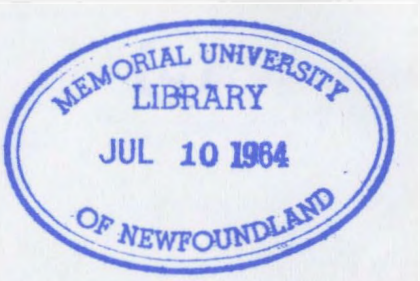
AGE DETERMINATION AND GROWTH-RATE OF REDFISH SEBASTES SP. FROM SELECTED AREAS AROUND NEWFOUNDLAND

E. J. SANDEMAN



AGE DETERMINATION AND GROWTH-RATE OF REDFISH SEBASTES SP. FROM SELECTED AREAS AROUND NEWFOUNDLAND.

by

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E. J. Samdeman

Abstract

This paper represents part of a continuing study of the distribution and biology of marinus and mentella redfish in the Northwest Atlantic. Reported here are the results of age determinations from the otoliths of mentella redfish from 5 areas around Newfoundland - Hermitage Bay, Southwest Grand Bank, Flemish Cap, Gulf of St. Lawrence and Hamilton Inlet Bank; and marinus redfish from Flemish Cap and Hamilton Inlet Bank.

The data from Hermitage Bay, in addition to providing information on the growth-rate of the redfish, have provided a means of appraising the basic method of age determination and it is concluded that the otolith method, as used here, is valid to ages of at least 10 years.

Growth of both marinus and mentella redfish was found to be adequately represented by the inverse exponential equation, and the parameters of the von Bertalanffy form of this equation were obtained by a least squares fit to the mean length at age values for males and females from each area.

The difference in growth-rate between the sexes was examined and it was found, as was expected, that the females showed a faster growth-rate than the males.

An examination of the growth curves and growth-rates of mentella from different depth levels on Hamilton Inlet Bank indicated that a considerable difference in growth pattern exists between fish from the shallower and deeper depths, and that the fish of the latter habitat tend to remain separate from those of the former, at least during the period of active growth.

Comparisons of the growth curves presented here with other published redfish growth curves reveal, in most cases, a basic agreement between workers using otoliths, and a disagreement between these workers and others who use scales for determining the age of redfish.

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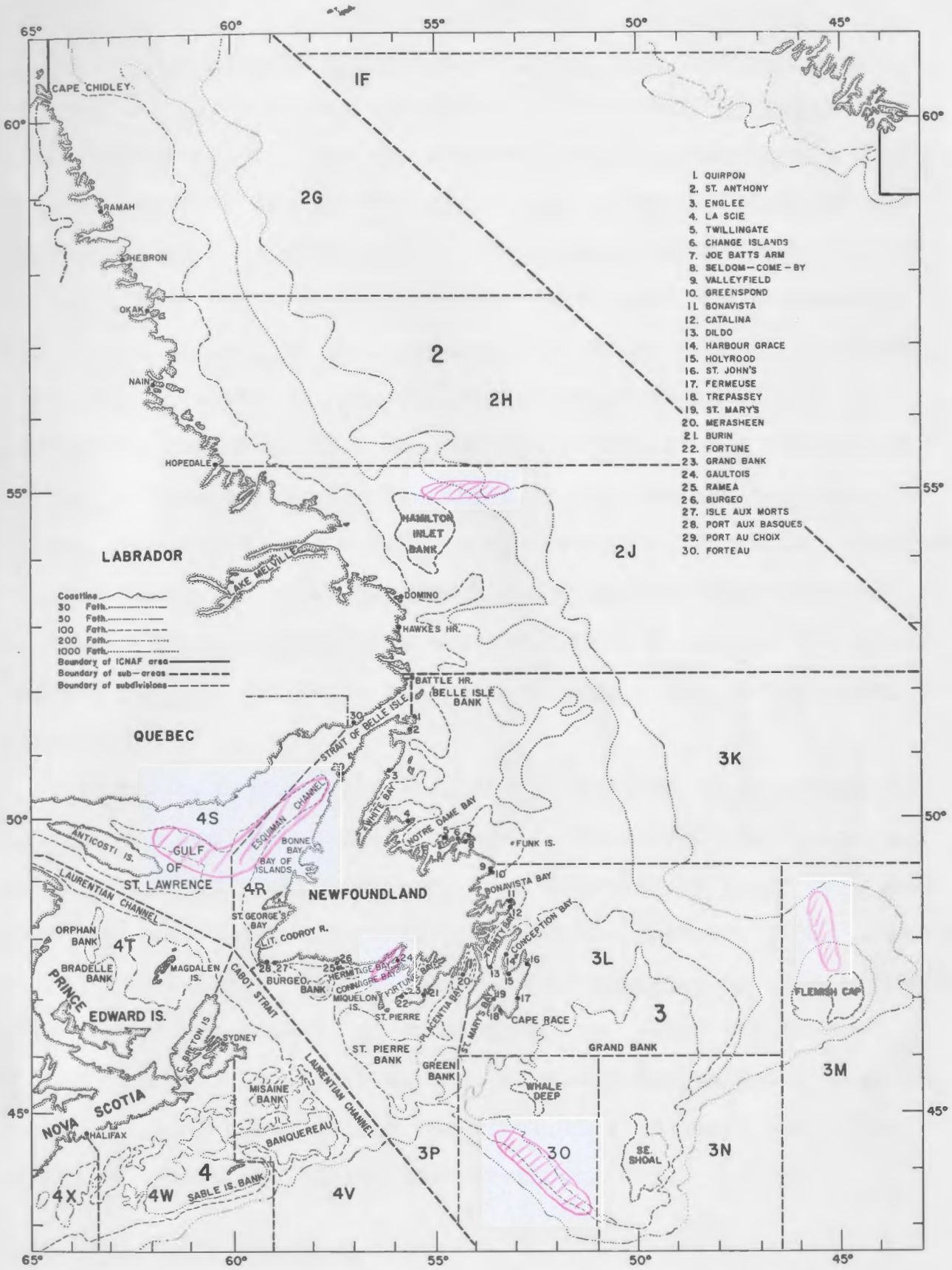

Figure 1.1 Map of the general Newfoundland area showing the localities from which samples were obtained. Also shown are the ICNAF Divisions.

1. INTRODUCTION

1.1 Redfish and their status in the Newfoundland area.

In the North Atlantic, redfish of the genus Sebastes are widely distributed. In the Northeastern Atlantic waters they range from the Barents Sea and Norway, to the waters off Iceland and Eastern Greenland, while in the Northwest Atlantic they are to be found from Davis Strait down the North American seaboard to the Gulf of Maine, as well as along the coast of West Greenland. (The area referred to here as the Northwest Atlantic may be defined as the convention area of The International Commission of the Northwest Atlantic Fisheries. The eastern boundary line of the convention area which, except near Cape Farewell, Greenland, extends along the 42° W. longitude line, divides this defined Northwest Atlantic area from what will here be called the north-eastern part of the North Atlantic or simply the Northeastern Atlantic.)

It has been customary to think of redfish as occurring only on and near the continental shelves. However it has long been known that even adult specimens were often to be found well away from land and above waters of great depths (Nansen, 1886; Murray and Hjort, 1912). Larval specimens of Sebastes sp. are extremely common over large areas of open ocean and, since the work of Collett (1880), many persons have observed how suitable plankton catching gear, when used at the right time of year, can often catch many hundreds of redfish larvae and fry.

1.11 Taxonomic position

The taxonomic position of the various members of the genus Sebastes in the North Atlantic is rather confused. In the

Northeastern area it is generally conceded that three different forms are to be found.

(a) Sebastes viviparus

This is generally regarded as distinct from its congeners in several features, and is allowed full specific status. Sebastes viviparus is usually found in the shallower coastal waters, particularly round the south and west coasts of Iceland, round the Faroes and Norway. The species does not normally occur west of the continental shelf off the western coast of Iceland, and only one specimen has been recorded from East Greenland waters (Kotthaus and Krefft 1957). Individuals of this species are usually under 35 cm in length and are of no commercial importance.

(b) Sebastes marinus

The common commercial redfish of the Northeast Atlantic waters prefers the shallower part of the redfish range. The distinction of this form from the mentella-form (below) has only been made in recent years, and even now fish may be encountered which appear intermediate between the two forms in one or more characters.

Current synonyms:-

Sebastes marinus = Sebastes marinus marinus = Sebastes marinus, marinus-type; referred to in this paper as "European marinus-type redfish".

(c) Sebastes mentella

The deep-water or beaked redfish, which are generally smaller than the marinus-type fish, were first noted by Lundbeck (1940), who referred to them as "Tiefenbarsch" or "Schnabelbarsch". Travin (1951) described these redfish in detail and provided the

Figure 1.2 Typical specimens of adult, male, mentella (upper) and marinus (lower) redfish from the Newfoundland area.

name above, but other workers have disagreed with the allocation of specific status.

Current synonyms:-

Sebastes mentella = Sebastes marinus mentella = Sebastes marinus, mentella-type; referred to in this paper as "European mentella-type redfish".

In the Northwest Atlantic, Sebastes viviparus is absent and the ecological niche that would be occupied by this species is filled by mentella-type fish, which may occur in depths from one to about 400 fathoms and thus appear more plastic in their depth range than their European counterparts.

(a) Sebastes mentella

The typical or common redfish of the Northwest Atlantic resembles, in morphometric and meristic features, the European mentella-type redfish, and the same synonyms are used in referring to it. However, it seems clear there are some differences between these European and North American forms and, until the systematic position is clarified, it seems best to consider them as separate forms. Thus in this paper I shall refer to them as "North American mentella-type redfish". As we are dealing principally with these fish, it is expedient to omit "North American", and refer to them as mentella-type redfish or simply mentella. Photographs of North American mentella and marinus may be seen in Fig. 1.2.

(b) Sebastes marinus

The presence in the Northwest Atlantic of a form of redfish resembling the "European marinus-type" was noted by Templeman and Sandeman (1957). These fish, which I shall call "North American marinus-type redfish" or just "marinus" apparently do not occur

in the southern part of the redfish range and may only be found north and east of the general line of Cabot Strait and Laurentian Channel. If they occur in a particular locality, they are generally to be found in the shallower part of the depth range occupied by mentella. They are not, however, very common and by far the greatest part of redfish catches from the area of the Northwest Atlantic south of Labrador are mentella.

There is no reason to suppose that the North American marinus are in fact different from their European counterparts, which are the main commercial redfish of Europe.

1.12 The distribution of redfish in the Northwest Atlantic

The distribution of redfish in the Northwest Atlantic has been described by Templeman (1959).

1.121 North American mentella-type redfish

Specimens of mentella have been taken as far north as Lat. 66°.47' N. on the American side of Davis Strait, where a single redfish was taken in a set made at a depth of 200 fathoms (Templeman, 1961). Southwards, off the coast of Labrador, they become more plentiful but it is not until the vicinity of Hamilton Inlet Bank is approached that they become sufficiently numerous to be caught in commercial quantities.

The most southerly reported catch of redfish on the eastern seaboard of North America is probably that of Goode and Bean (1895), who report catching a redfish in a depth of 114 fathoms at Lat. 39°.48'.10"N. Long. 71°.48'.40".W. The most southerly concentrations of breeding redfish are said by H. W. Graham to be in the South Channel between Nantucket Shoals and Georges Bank (Templeman, 1959). No distinction has been made, in the case of these southern records, between mentella and marinus, but from our

own studies of the redfish of the Nova Scotian Shelf, it seems certain that these fish were of the North American mentella-type.

Between the northern and southern limits lies a vast area of potential redfish habitat, and indeed redfish may be found at suitable depths over almost the entire area. A relationship between redfish distribution and depth and temperature was first proposed by Tåning (1949), who concluded from a study of the distribution of Sebastes larvae that redfish were not plentiful except in areas where temperatures between 3°C and 8°C exist in depths of about 200-500 m. (110-270 fathoms). Templeman (1959) carried the study of this relaticnship to the distribution of redfish as caught by otter trawls on the sea bottom, and besides agreeing with Tåning's general conclusion, was able to narrow the generalisation to the range of 3°C to 6°C, or at least to areas where temperatures of 3°C to 6°C are present in redfish depths for a large portion of the year.

Templeman (1959) was also able to show that, in general and within the temperature range suited to redfish, depth is more important than temperature in the vertical distribution of mentella and marinus. He was able to demonstrate that the occurrence of marinus as the common redfish of Europe and mentella as the common redfish of North America was explainable by a simple hypothesis based on the preferred temperatures and depths of the two types.

1.122 North American marinus-type redfish

Being so very much less abundant than the mentella of the area, the northern and southern limits of distribution are not so well known. Three marinus were caught by the research vessel A. T. Cameron at 65°.08'.30"N. 58°.10'.W . and depth of 300 fathoms

in August 1959 (Templeman, 1961). On the West Greenland side of Davis Strait, marinus redfish occur in commercial quantities as far north as about 69°N. (Travin, Janoulov, Postolaky and Zaharov; 1961). Jensen (1926) states that specimens have been noted as far north as 71°N.

The most southerly occurence that we are aware of is, for marinus, around the "tail of the Grand Bank" (about 43°N.). Fishing by the A. T. Cameron on the Nova Scotian Banks has not, as yet, revealed any marinus in this area.

In general, marinus can be regarded as preferring the shallower part of the redfish depth range and, if they are present in an area, their depth of greatest abundance is usually at a shallower depth than the depth of greatest abundance of the mentella. This pattern of depth distribution can be completely disorganised during the period of larval extrusion, when the available evidence points to a migration of extruding fish to deep water. There is some evidence that, in the Newfoundland area at any rate, they prefer a more rocky type habitat than do mentella.

1.123 Bathypelagic stocks of redfish

It has been known for some time that redfish are pelagic and not demersal in their feeding habits (Idelson, 1930; Boldovski, 1944). Subsequent workers have shown that this is not only true for European marinus-type redfish, on which we must presume the work of these earlier authors to be based, but also for North American mentella-type redfish (Templeman, 1954; Steele, 1957; Lambert, 1960; Kashintsev, 1962) and for North American marinus-type (Kashintsev, 1962). It is thus not very surprising to find that redfish may be present in the open ocean as a bathypelagic stock, apparently living their lives completely

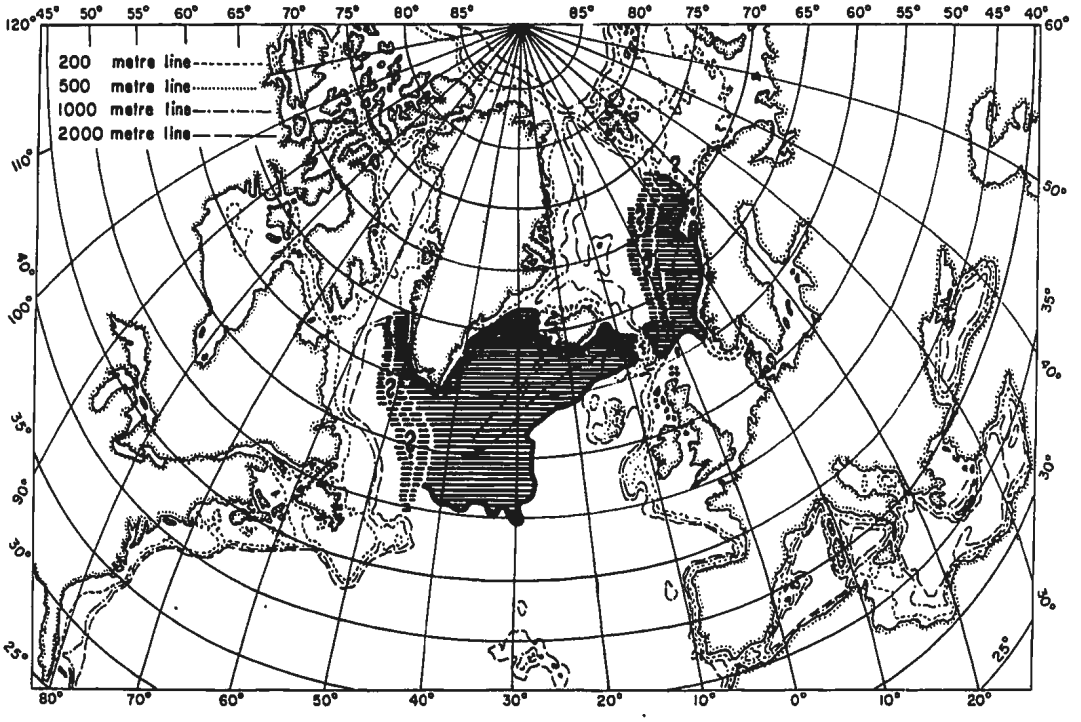

Figure 1.3 Distribution of larvae of Sebastes marinus in the central and eastern North Atlantic. (After Tåning, 1949, fig. 4)

divorced from the sea bottom.

Since the earlier observations of Nansen (1886) and Murray and Hjort (1912) of redfish occurring away from land and over water of great depth, most research on the possibility of oceanic stocks has, until recent times, been concentrated on the occurrence and distribution of larvae. The work of Tåning (1949, 1951) and later Einarsson (1960), Hansen and Andersen (1961), Henderson (1961a, 1961b, 1962 and MS, 1963) and many others has shown that the larvae of redfish are, during May to July, extremely common over the area of the Irminger Sea and indeed over a large part of the North Atlantic Ocean (Fig. 1.3). Raitt (MS, 1962) has calculated that in the eastern part of the Irminger Sea, between 16 and 40 million redfish larvae could be present under each square kilometre of sea surface. Henderson (1961) suggests a figure exceeding 100 million larvae under each square kilometre for the most prolific areas in April and May, and considers this figure to be minimal.

The large numbers of larvae that have been found across the open ocean suggest a very large bathypelagic population of adult redfish, or a mass migration of females to the areas of open ocean to extrude their larvae. It is only very recently that any light has been shed on this problem, and results of particular interest are to be found in the works of Henderson (MS, 1963) and Zakharov (MS, 1963).

Henderson (MS, 1963) reports results obtained by hook and line fishing from ships at Ocean Weather Station "A" (Lat. 62°N. Long. 33°W.). Although the catches were not large, some redfish were taken in fishing attempts over a large part of the year.

In spite of the fact that of the 30 specimens which were returned to the laboratory only 3 were males, the results are indicative of a resident population in the area rather than a concentration of females present solely for larval extrusion.

Zakharov (1963) was able to obtain numbers of adult redfish (usually 1-4 per set) by use of a pelagic trawl over almost the whole area of the Irminger Sea. The most interesting point made in both these papers is that the redfish caught in the bathypelagic part of the North Atlantic were all mentella-type (there were a few intermediate type fish) in morphological form, and because the larvae they produce are more similar in their lack of caudal melanophores to the European mentella-type than to the North American mentella-type, we must class them, provisionally at any rate, as the former. It is significant that Zakharov obtained both males and females and, although the fish were all large (32-48 cm), both mature and immature fish were present.

1.13 Reproduction of redfish

Redfish differ from most other commercial species of fish in that they are viviparous. In oviparous fishes, the spawning period is a time when the males and females come together to shed and fertilize the eggs and when very large schools are often formed, thus providing one of the great opportunities for man to harvest vast quantities of fish. In the case of redfish the "spawning perio is actually an "extrusion" period when the small well-developed larvae are liberated. At this time the presence of males is not required and schools of "extruding" females may be formed. There is some evidence that such schools are sometimes formed in deep water (250 - 350 F.), but whether or not the birth of the larvae

takes place at these depths is not known.

The time when fertilization takes place must of course come earlier, before the development of the larvae in the parent is started. Our own work, as well as that of Magnusson (1955) and Sorokin (1958, 1961), has shown that the period of sperm transference (copulation) occurs several months before the eggs are activated and development of the ova starts. Sperm may be found in the ovary from the time of first copulation. Whether these sperm are just being stored for later fertilization of the eggs, or whether the developing oocytes have been already fertilized and these sperm are those superfluous to requirements, is not fully understood. Sorokin (1958) has presented some evidence pointing to the conclusion that the sperm are passively stored in the ovary until a change in pH concentration of the ovarian fluid triggers their activity, resulting in fertilization and activation of the ova.

In the Newfoundland area, copulation generally occurs in the period August-September-October with larval extrusion occurring about April-May-June for mentella. For marinus the time of copulation could be considered rather similar, but some evidence exists that, in some areas at any rate, the time when larval extrusion occurs is earlier by a few weeks than that of mentella (Templeman and Sandeman, 1959).

1.2 Age and growth studies in fish

Of all the various aspects of the biology and life-history of a species of fish, one of the most important is that of growth. The relative growth rate can, in certain populations, be studied without direct referrence to age.

However, in any critical study, reference to age is required, and thus for most purposes, obtaining the ages of individual fish becomes the prerequisite for growth-rate studies as well as many other aspects of the life history: age at first maturity, average age at first capture by a fishing gear, age composition of the population, longevity and others.

1.21 Methods of Age Determination

In general, two methods are open to the fisheries biologist who wishes to determine the ages of samples of a population of fish.

1.211 Petersen's Method

This method makes use of the polymodal nature of the length frequency distributions of samples containing more than one age group. Because most marine commercial fishes have a single rather restricted annual spawning season, and because the lengths of the individuals resulting from each spawning season tend to be normally distributed, it is often possible, particularly in the early years of a fish's life, to obtain mean lengths for the various year-classes, each of which is represented by a mode in the polymodal length frequency distribution.

Petersen used this technique for studying the seasonal and annual growth increments of plaice before the more direct method of age determination (below) had been established and, in general, the direct methods have largely replaced it. Petersen's method still provides a useful way of verifying the validity of the more direct methods of ageing fish and has been used by redfish workers for this purpose.

1.212 Use of skeletal structures

Most fishes which live in the oceans of the temperate zones are subject to seasonal climatic changes, and although these changes may not appear to influence the external environment of the fish directly, they do exert some effect which usually may be seen in a correlated cycle of change in the internal environment of the fish resulting in an increase in metabolism and growth during the summer and slow growth during the winter. This fluctuation in growth rate is reflected in all the hard parts of the fish. Examination of the skeletal structures of such fish will show the alternating bands of fast and slow growth.

This method of ageing fish was used as long ago as 1759, when a clergyman in Sweden aged several species of fish (including cod) by counting the marks on the centra of the vertebrae (Hederström, 1759). The method was then largely forgotten till it was rediscovered and critically tested by Hoffbauer (1899) who described how the age of carp could be determined from its scales. Following Hoffbauer's paper, a great number of workers examined the scales of many species, and after quite a controversy between several of the senior biologists of the time the method finally became established. Van Oosten (1929) and Graham (1929) have provided a very complete review of the general method, with emphasis on the use of scales, and according to them otoliths were probably first used by Reibisch (1899).

If skeletal structures are to be used for age determination, it is essential that the validity of the method used be established for the species, and often as well for the area in which the population being studied lives.

1.213 Other Methods

Several other possible methods of ageing, or at least of examining growth rates, have been used, but with the general acceptance of the method using skeletal structures, and more particularly scales and otoliths, these other methods have been largely relegated to auxiliary status and have their main use in establishing the validity of the method used. Included here might be mentioned such techniques as - marking and recapture and aquarium studies.

1.22 The mathematical description of growth.

From a study of the ages and age structure of samples from a given population of fish, we may derive two basic quantities; one represents the sizes of the fish and the other the ages or time required for the fish to attain these sizes. If these two basic quantities are plotted graphically against each other, and if they prove to be mutually dependent within the limits of the units used, the graphical plot will approximate to a curve. The curve resulting from the plot of size against age is defined as the growth curve. (The functions of size most usually studied in fish are those of weight and length.) If a growth curve can be drawn and the variables prove to be mutually dependent, it is convenient to further analyse the relationship between the variables and summarise the relationship explicitly in the form of a mathematical equation.

Once derived, an equation of growth can greatly facilitate the analysis of the growth-curve, as well as make immediately available all the material which can be extracted from it by simple mathematical manipulation.

Also, in this era of mathematical models and computers, it is necessary to summarise the growth function mathematically, so that it can be easily incorporated into the wider model to provide an insight into the inter-relationships of the study animal with other animals and even man.

Many different equations have been used in studying the growth of animals and plants. (Summaries may be found in Gray, 1929; Medawar, 1945; and more specifically for fish, Beverton and Holt, 1957*). Most of these equations have been purely emipirical, and although they are usually found to fit the data adequately, their parameters do not lend themselves to any physiological interpretation and the "good fit" appears merely fortuitous.

1.221 The von Bertalanffy growth Equation.

One of the most convincing attempts at providing a physiological basis for a growth equation was that of Ludwig von Bertalanffy (1934, 1938, 1949 and 1957). He recognized growth to be the resultant of the two general body processes, that of anabolism or building up and catabolism or breaking down, and derived a growth equation from the continuity relation

$$\frac{dw}{dt} = Hs - kw \quad \ldots\ldots\ldots\ldots\ldots\ldots \quad (1)$$

*Of particular interest are papers by Richards (1959) and Taylor (1962) who consider the complete family of the most usual growth curves and show how they are related to each other.

This differential equation states that the increase in weight per unit time, $\frac{dw}{dt}$, is equal to the weight synthesized per unit surface area, H, times the total surface area, s, less the destruction per unit weight, k, times the total weight, w.

Ludwig von Bertalanffy assumed that the area of surfaces involved in anabolic processes is proportional to the square of a linear dimension, and that the weight related to the catabolic processes is proportional to the cube of the linear dimension.

$$s = pl^2$$
$$w = ql^3$$

where l is length and p and q are constants of proportionality.

Substituting in (1) $\frac{dl}{dt} = \frac{Hp}{3q} - \frac{k}{3} l = E - Kl$ ..... (2)

where $E = \frac{Hp}{3q}$ and $K = \frac{k}{3}$

Integration of equation (2) leads to the von Bertalanffy (hereafter called the Bertalanffy) growth equation.

$$l_t = \frac{E}{K} - \left(\frac{E}{K} - L_o\right)e^{-Kt} \quad \text{..... (3)}$$

where "L_o" is the length of the organism at zero age and "e" is the base of natural (Naperian) logarithms.

As "t" becomes large "l_t" approaches "$\frac{E}{K}$" as the limit "$L\infty$" (which is the asymtotic length, the greatest possible length that the organism under the given conditions can attain).

$$l_t = L_{oo} - (L_{oo} - L_o)\, e^{-Kt} \quad \ldots\ldots\ldots \quad (4)$$

It is convenient to consider $L_o = 0$ when $t = t_o$ and equation (4) then becomes the more usual form.

$$l_t = L_{oo}\, (1 - e^{-K\,(t - t_o)}) \quad \ldots\ldots\ldots \quad (5)$$

The corresponding equation for growth in weight may be derived by substituting w in terms of l in the above equation.

$$w_t = W_{oo}\, (1 - e^{-K\,(t - t_o)})^3 \quad \ldots\ldots\ldots \quad (6)$$

The basic Bertalanffy equations (5) and (6) have been shown by many authors (particularily Beverton and Holt, 1959), to adequately represent the growth of many species of fish and it is this type of equation that has been fitted to our age-length data of redfish.

Several interesting points arise from a consideration of the basic equation:

$$l_t = L_{oo}\left\{1 - e^{-K\,(t - t_o)}\right\}$$

(a) By simple algebraic manipulation the following simple relation can be derived.

$$l_{t+1} = L_{oo}\, (1 - e^{-K}) + l_t e^{-K}$$

where l_{t+1} represents the length at age $t+1$ years.

This equation is that of a straight line, and the property of a straight line being obtained by the plot of l_t against l_{t+1} was discovered independently by Ford (1933) and Walford (1946).

This transformation of the Bertalanffy equation to a linear form is utilized in some of the methods used for fitting the Bertalanffy equation to a set of age length data (Beverton and Holt, 1957; Ricker 1958).

(b) It is important to ponder just what the various constants mean. L_{oo} represents the final size (asymptotic length) to which an individual under specified conditions can attain, or when approached from the population standpoint, the average final size a sample of the population would attain, again under specified conditions. K is a parameter expressing the relative rate of approach to L_{oo} and t_o is in reality only a scale constant, the theoretical age at which l_t and W_t are equal to 0.

From the physiological standpoint $L_{oo} = \frac{E}{K}$ where E is the coefficient of anabolism and $K = \frac{k}{3}$ where K is the coefficient of catabolism.

Beverton and Holt (1957) regard K as independent of changes in food consumption, and represent changes in growth-rate by appropriate variation of the parameter W_{oo} or L_{oo}. Taylor (1958, 1959 and 1960) has presented some evidence to show that K increases with increasing temperature in cod (Gadus morhua), in the Pacific razor clam (Siliqua patula) and the Pacific cockle (Gardium corbis). However, as has been pointed out by Holt (1962), the method used by Taylor for determining the constants K and L_{oo} (plot of

l_{t+1} against l_t) might well lead to a spurious correlation between E and K, for a small chance rotation of the line around its mid point will simultaneously result in lower K and higher L_{oo} values or vice versa. This apparent inverse correlation between K and L_{oo} has been remarked on by several authors and indeed, it is not surprising that such a correlation exists, for as Knight (M.S., 1962) has shown the correlation is in fact a mathematical consequence of the model, as can be seen below.

The Bertalanffy equation (4) is taken as the starting point

$$l_t = L_{oo} - (L_{oo} - L_o)\, e^{-Kt}$$

$$l_{t+1} = L_{oo} - (L_{oo} - L_o)\, e^{-K(t+1)}$$

Subtracting and rearranging terms we get.

$$l_{t+1} - l_t = e^{-Kt}\,(1 - e^{-K})\,(L_{oo} - L_o)$$

For convenience let us take time zero not as the time of birth, but as the time when Bertalanffy growth becomes applicable. Thus putting $t = 0$ and $l_{t+1} - l_t = G$ we get.

$$G = (1 - e^{-K})\,(L_{oo} - L_o)$$

which may be rearranged to give.

$$L_{oo} = L_o + \frac{G}{(1 - e^{-K})} \quad \text{..... (6)}$$

where L_o is the length of the organism at the time when Bertalanffy growth becomes applicable and G is the increase in length between L_o and the length one year after.

(c) It is apparent that in the Bertalanffy growth equation we have a growth formula describing a growth curve with no parameter of growth-rate. Growth-rate is a technical term which is usually used rather loosely. Often, when talking of growth as it concerns populations of fishes, it is said that fish from one area grow faster than fish from another, merely because at a given age the fish from the former area are bigger on the average than those from the latter. While the statement is true, in this case, over the total period in question, the implication that it is true over all the sections of time which make up the total period is not correct.

The growth-rate, which in a plot of age against size is represented by the slope of the curve at each instant of its generation, is, in Bertalanffy type growth, continually changing, and when length is plotted against age the growth-rate will start fast and gradually diminish as the asymtotic length is approached. In growth which follows the pattern of the Bertalanffy equation (4 or 5), the growth-rate is directly proportional to the length of the organism, as can be seen from equation (2) in the derivation of the above formula.

$$\frac{dl}{dt} = E - Kl = KL_{oo} - Kl \quad \ldots\ldots\ldots\ldots \quad (7)$$

To obtain the growth rate in terms of time rather than length, the original Bertalanffy equation may be differentiated to yield

$$\frac{dl}{dt} = KL_{oo}e^{-K\,(t-t_o)} \quad \ldots\ldots\ldots\ldots\ldots \quad (8)$$

In both these equations $\frac{dl}{dt}$ represents the instantaneous growth-rate. The above equations provide a convenient means of comparing the growth-rates of two or more populations having different parameters K, L_{oo} and t_o. Using equation (7), and considering a plot of $\frac{dl}{dt}$ against l, we should obtain a straight line having the intercept on the y axis of KL_{oo} and on the x axis of L_{oo}. Thus if the Bertalanffy equations of a series of growth curves are available, the differences in growth-rate between them can quickly be seen by plotting KL_{oo} on the y axis and L_{∞} on the x axis and joining them to provide the plots of $\frac{dl}{dt}$ against l for each individual growth curve. The straight lines should of course be drawn only for the values of l for which actual data is available.

In similar manner a semilogarithmic plot of $\frac{dl}{dt}$ against t for equation (8) can be used for comparing growth-rates and how they change throughout the lives of different organisms, viz.

$$\log \frac{dl}{dt} = \log K + \log L_{oo} + Kt_o - Kt$$

and in this case the y axis intercept would be ($\log K + \log L_{oo} + Kt_o$) and the x axis intercept $\left(\frac{\log K + \log L_{oo} + Kt_o}{K}\right)$. Again the straight lines should only be drawn for the ages from which the Bertalanffy parameters have been derived. Although the former plot (equation (7)) is very much simpler, it is deceptive in that it is more customary to think of growth-rate in terms of age rather than length. Consequently in the comparisons of growth-rates presented here it will be most often the latter equation that will be used.

1.222 Methods of fitting the Bertalanffy growth equation.

The method which is most often used to obtain estimates of the parameters of the Bertalanffy growth equation is that described by Beverton and Holt (1957). In this method the Ford-Walford transformation is utilised and the plot of l_{t+1} against l_t or $W_{t+1}^{1/3}$ against $W_t^{1/3}$ provides estimates of K and L_{oo} or W_{oo}. An estimate of t_o is obtained by converting the usual Bertalanffy equation to its related form (linear in t)

$$\log (L_{oo} - l_t) = \log L_{oo} + Kt_o - Kt \quad \ldots (9)$$

and plotting $\log (L_{oo} - l_t)$ against t. This yields a straight line of slope K and intercept ($\log L_{oo} + Kt_o$), from which the theoretical age at which the length of the fish is zero, (t_o) may be calculated.

Ricker (1958) is critical of the above method, because in setting the Walford line to the data, both ordinate and abscissal values are subject to sampling error causing the points to lie

erratically with respect to the line fitted, and also because the two terminal values are used only once while all others are used twice. He prefers to utilise the Walford plot to obtain an approximate value for L_{oo} from a freehand curve and then to use this trial value in the expression (9) above. A graph of log $(L_{oo} - l_t)$ against t should be straight and the straightness is sensitive to changes in L_{oo}. By making a few trial plots the L_{oo} which gives the best (straightest) line can be found, and this line immediately determines K and provides an estimate of t_o.

Another and very simple but inaccurate method which also uses the Ford-Walford transformation is discussed by Knight (MS., 1962). The data are divided into four consecutive groups of equal size (if the data are not divisible by four, observations are discarded from the middle). The average length is computed for each group, and from these averages a three point Walford diagram is plotted and a Walford line drawn through the end two points. The slope of the line is K^n where n is the number of observations in each group, and L_{oo} may be obtained directly from the intersection of the Walford line with the 45^o line.

If we wish to compare the growth curves and growth rates of different populations of fish, it is necessary that an objective method be used to determine the parameters of the different equations of growth. In examining the methods discussed above, it is immediately apparent that Ricker's method is subjective, and the values of the parameters obtained can depend purely on the judgement of the operator. The last method is obviously very inaccurate and Beverton and Holt's (1957) method is open to the criticisms leveled by Ricker (1958) and Holt (1962).

In addition, a further disadvantage of the Beverton and Holt method became apparent when we started using the method for obtaining growth equations for redfish. In the virgin populations of redfish, which we were studying, the greatest part of our length at age data occurred at old ages and large sizes, where the asymptotic part of the curve was being approached. Because of this, negative values of $(L_{oo} - l_t)$ occurred quite frequently and this affected the second stage of the fitting process when we were unable to obtain values for log $(L_{oo} - l_t)$ when $(L_{oo} - l_t)$ was negative.

The above disadvantage could have been obviated by grouping the data or applying an extensive system of smoothing, but in the interests of greater objectivity the method was not used.

A further disadvantage of the three methods that have been discussed above is that, although they provide estimates of the parameters of the Bertalanffy equation, they do not provide any estimates of the reliability of these parameters. Knight (MS, 1962) has described a modification to the technique of fitting a least squares line to the Walford diagram but the method requires that e^{-K} approaches one.

Stevens (1951) has considered the application of least-squares techniques to the general regression equation $y = a + Bp^x$ (the basic family to which many proposed growth curves belong - Gompertz, logistic and Bertalanffy among others) and developed an iterative procedure for fitting this equation. If the values of the independent variable (in our case "ages") are equally spaced, he showed that tables could reduce the arithmetic load in calculating the covariance matrix, and provided tables to aid in the computation of this matrix for five, six and seven equally spaced values of x.

Pimentel Gomes (1953) extends Stevens' work above and his own previous work (Pimentel Gomes and Malavolta, 1949) in a paper concerned with Mitscherlich's regression law and its application in experiments with fertilisers. In this paper he describes a procedure for estimating the parameters of the curve

$$y = A\,(1 - 10^{-c(x + b)})$$

by the method of least squares and follows Stevens' (1951) method in deriving the variances of the parameter estimates from the covariance matrix.

Iterative techniques, especially when convergence is slow, can be extremely tedious, and unless access is available to a computer some shortening of the iterative process is desirable. This is in effect what was done by Pimentel Gomes (1953) who, by incorporating a constant time interval between each value of the independent variable and considering a constant number of observations at each of these values, was able to eliminate the bulk of the tedious iterative calculation in favour of the solution of a polynomial using a set of tables.

This method of Pimentel Gomes (1953) was extended to fit a form (Beverton, 1954) of the Bertalanffy equation for growth in length by Tomlinson and Abramson (1961), and it is this method that has been used throughout this paper.

Like the method of Pimentel Gomes (1953) the method of Tomlinson and Abramson also requires that the values of the independent variable (ages) be equally spaced, and that there are a constant number of measurements within each (age group).

If these conditions are fulfilled it is possible to compute tables to assist in solving a polynomial which yields on solution an estimate of the parameter K. Tables have been computed by Tomlinson and Abramson for up to 18 age groups, and these are used to find the solution to the polynomial by successive trials. Once the parameter K is determined it requires only simple algebra to substitute this value in the normal equations of the function to obtain least squares estimates of L_{∞} and t_o. When an equal number of observations in each age group are used a true least squares line is obtained if the variances of the length at age values are equal.

Usually a collection of age-length data does not contain an equal number of observations from each age group, and in this situation Tomlinson and Abramson suggest that either equal sized random samples be selected from the age-groups containing a sufficient number of observations, or all the data may be used. In the latter instance a weighted least squares fitting procedure is appropriate, and recourse must be made to a complete iterative procedure without the convenience of tables.

To select equal sized random samples means, in effect, discarding data, and with the variation that is apparent in the redfish length at age data this was undesirable. On the other hand, it was impracticable to undertake the vast amount of iterative computation that would be involved in the weighted least squares fitting procedure. It was decided to make the most use of the best data available and to undertake the least squares fit on the unweighted data.

Thus instead of the least squares fit to the individual points at which length is expressed in terms of age, least-squares fits to the mean lengths at each age only have been considered in this paper.

One of the advantages of these methods of fitting the curve directly, as opposed to fitting by approximation through transformation, is that the direct methods can provide estimates of the variances of the parameters. These variances can be determined from the elements of the covariance matrix (formed when the basic information matrix of sums of squares and products is inverted) together with the residual variance. The distribution of the estimated parameters is, in general, unknown and caution is needed in interpreting the variances. Because the least square fits have been made to unweighted mean length data rather than to an equal number of observations at each age, the variances which we might obtain for the parameters of the fitted equations must be considered maximal, and refinement of the fitting procedure will in general provide lower variances.

The use of a weighted fit least-squares technique would lead to a more rigorous fit and better variance estimates. It is interesting to note that Abramson (1963) has supplied a computer routine for fitting the Bertalanffy length curve to age and length data from 30 or fewer age-classes. Neither equal time intervals between ages nor equal numbers of lengths at each age are required. However the number of lengths for each age group must be at least two and at most 600. The output includes estimates of L_{oo}, K and t_o, their standard errors, and fitted lengths from zero to the maximum in the sample. The estimates are accurate to at least four significant figures, and execution time for a single curve is less than 15 secs.

1.3 Age determination and growth-rate in redfish

The first information on the likely growth rate of redfish is to be found in the work of Jensen (1922). From a study of the sizes of larvae and fry in different months, Jensen was able to deduce that young redfish would be about 47 - 69 mm in length by the winter of their first year. He suggested, on the basis of length frequency data which he admitted was rather limited, that the fish in age group I would be 7 - 17 cm in length, age group II, 19.5-30 cm and age group III, 31 - 41 cm in length.

Saemundsson (1932) stated that redfish reached sexual maturity at a length of 40 cm, at which time they were 8 to 10 years old.

To Smaragdova (1936) can be credited the first detailed account of age determination in the genus Sebastes. A total of 766 determinations were made from scales and 69 parallel determinations from otoliths taken from redfish from the general area of the Barents Sea. Smaragdova found it easier to determine the age by otoliths than by scales, but obtained excellent agreement between the two methods. He found that ages of 1 - 27 years were present in the samples and that the growth-rate was rather slow. From the fact that fish were present to a length of 57 cm, it seems likely that these redfish were of the European marinus-type.

In 1944, Veschezerov published the results of his investigations into the growth-rate of redfish from the Barents Sea. After examining a variety of the bony parts of redfish including otoliths, cleithra, opercula and vertebrae, Veschezerov concluded that scales were the most satisfactory for age determination. He presents an age-length and age-weight key derived from the scale

readings of 377 redfish between the ages of 9 and 24 years caught on the western slope of Murmansk Bank and Finmark Bank. An age-length key for younger redfish (1-10 years) he derived from backcalculation of scales from a special sample of 53 sub-commercial sized fish. Veschezerov's data agreed quite closely with the slow growth-rate obtained by Smaragdova. Because of the large size of most of the fish and the shallow depths from which many of the samples were obtained, it is most likely that Veschezerov like Smaragdova was dealing with European marinus redfish.

During the years 1938 to 1941 Kotthaus had been working on the problem of age determination in redfish, and due to the intervention of the war he did not publish his results till 1949. At the time of his first paper (Kotthaus, 1949) he was unaware of the earlier work of the Russian workers Smaragdova and Veschezerov. He did however take issue with some unpublished work of Fridriksson and Kunne both of whom, using otoliths, had expressed the opinion that redfish were slower growing than most other commercial marine fish (Kotthaus quotes a personal communication from Fridrikkson who found that in a sample of 85 redfish from Icelandic waters, there was one four-year old, 11 cm; 10 five-year olds, 12 - 14 cm; 69 six-year olds, 13 - 19 cm; and 5 eight-year olds, 16 - 19 cm.)

Kotthaus argued that, although very many rings may be observed in the bony structures of redfish and in particular on the otoliths, only one out of about every three is really distinct and it is only this distinct ring which must be counted to provide an estimation of the age of a fish. This procedure naturally reduced the ages as determined by Kotthaus by a factor of about three, and whereas other earlier workers had obtained ages of

of 23 and 24 for fish about 57 - 60 cm, Kotthaus considered fish of mean length 56.6 cm to be only seven years old.

This thesis of a relatively fast growth-rate was developed further by Kotthaus in an extended paper in 1952 (Kotthaus, 1952).

The first published attempt at an age and growth study of the redfish of the Northwest Atlantic was by Perlmutter and Clarke (1940). These authors used the scale method but, because the scales were not clear to read when the fish were greater than about 24 cm in length, they confined their study to the smaller and younger fish of the population. With a cut-off size of 23.5 cm, by far the majority of the fish studied were immature. Perlmutter and Clarke made a serious attempt to validate their method and they suceeded in showing that, at least during the early life of the fish from the Gulf of Maine, a single zone of narrowly spaced circuli was laid down in the period November to March of each year. This study showed a very slow growth-rate for redfish in the Gulf of Maine.

Travin (1951) described the new species, the deep-water redfish Sebastes mentella, and in pointing up the differences between it and the normal common redfish of Europe, Sebastes marinus, showed growth data for both these forms. Travin's ages were obtained from scales (personal communication) and only average lengths at each age are presented. These data indicate that they grow at about the same rate to about 4 years of age, and after this mentella grows more slowly until at about 17 to 18 years the marinus fish average 8 to 9 cm longer than the mentella-type.

In 1956 a symposium was convened by the International Commission for the Northwest Atlantic Fisheries (ICNAF) in which it was proposed to examine several of the current "problems" of fisheries biology. Included among them was the problem of the ageing of redfish. Papers, individual otoliths and other materials helpful to the problem were all discussed. Dr Kotthaus presented a written contribution outlining the main arguments underlying his general thesis of a fast growth-rate (Kotthaus, 1958). Mr Kelly then presented the alternative viewpoint of the slow growth-rate (Kelly and Wolf, 1958, 1959). In his presentation, Mr Kelly showed some excellent photographs of redfish otoliths taken from fish of the Northwest Atlantic. All these showed clearly defined hyaline zones between which no sound reason for discounting some and counting others could be found. These age readings indicated a very slow growth-rate in Sebastes.

Additional evidence in favour of the slow growth rate hypothesis was presented by Rasmussen (1958), who presented and discussed some excellent photographs of otoliths from Sebastes marinus and Sebastes viviparus, and by Dr. Templeman who presented length frequencies of a group young redfish from Hermitage Bay on the south coast of Newfoundland. This group of fish, well isolated in length from the larger fish which composed most of the catch, was followed during 8 research cruises in 1954 and 1955. The scales from these fish, which showed an incomplete first year when they were first captured in December, 1953, showed 1 year in December 1954 and 2 years in November 1955. (Sandeman 1957, 1958).

Although not recorded in papers, two further significant contributions are noted by Parrish (1958), the convener of the group studying the problem. Dr G. Rollefson presented photographs of otoliths prepared by Norway and claimed that it was impossible to discriminate between the two types of zones as claimed by Dr. Kotthaus. The Norwegian age interpretations agreed substantially with Mr. Kelly's. Dr. Fridriksson cited examples of Sebastes otoliths on which up to 70 winter zones could be counted, and announced he was forced to regard Sebastes as a very slow-growing fish.

The general opinion of the group was that the wide divergence in growth-rates obtained by adherents to these two schools of thought was, for the most part, due to basic differences in the method of interpreting the zones of the otoliths. The group noted also that, several times during the meetings, information was presented which illustrated substantial differences in growth-rate between stocks of Sebastes in different parts of the North Atlantic, and recognised that progress in the racial problem was required before real differences in growth-rates between stocks of fish and between age-reading techniques could be elucidated.

The next great landmark in redfish research was a five day symposium devoted entirely to redfish. This was held in Copenhagen in October 1959. Before this meeting, however, several important papers on redfish ageing and growth-rate were forthcoming. Bratberg (1955, 1956a, 1956b) undertook a careful study which validated the use of scales and otoliths for age determination in redfish obtained from three localities along the coast of Norway.

Steele (1957) in a biological study of the redfish of the Gulf of St. Lawrence published growth rates of male and female redfish from the otoliths of a sample of 101 fish. Surkova (1957) examined a total of 4119 mentella-type redfish for age investigations using scales. These redfish were caught in the Barents Sea in the years 1953, 1954 and 1955. She obtained a growth-rate for mentella-type redfish from the Barents Sea rather similar to that obtained by Travin (1951).

Kelly and Wolf (1959) added a significant contribution to the literature on Sebastes of the Northwest Atlantic. This paper was in fact an expanded version of Mr Kelly's presentation to the 1956 symposium, and the complete paper was preceded by several minor informative articles or abstracts (Graham, 1953, 1954, 1955, 1956 and 1957; Anon 1957). In this paper Kelly and Wolf present conclusive evidence that both on otoliths and scales, one and only one hyaline layer or annulus is laid down per year. Their growth curves show an extremely slow rate of growth for the redfish of the Gulf of Maine.

In 1956 the vanguard of the great Russian fishing fleet arrived in the waters of the Northwest Atlantic and whereas in 1955 they had not a single vessel fishing for redfish in the ICNAF area, by 1959 their catch had risen to 155,000 metric tons, a figure greater than the amount landed from the area by all countries put together in any one year prior to 1956. This great fishing effort was accompanied by research effort as well, and the results of age determination by Russian workers of the redfish of the Northwest Atlantic began to enter the literature with the publication of age distribution data (Marty, 1958; Travin 1959).

At the Redfish Symposium in Copenhagen held in October 1959, several papers on the ageing and growth-rate of redfish were presented, and once again most of these presented evidence supporting the slow growth-rate hypothesis.

Hansen (1961) summarised his work on small redfish from Godthåb Fjord, Greenland (Hansen 1957, 1958a, 1958b, 1958c, 1959). He was able to sample a population of small redfish 46 times between July 1946 and June 30th 1959. The majority of the redfish were below 25 cm in size and Hansen was able to apply Petersen's method and obtain both ages and growth-rates for different year-classes to an age of about 7 - 8 years. He found the growth-rate to be very slow (20 cm in 6 years).

Kelly, in addition to presenting the previously published paper (Kelly and Wolf, 1959), gave an extremely interesting paper on their studies of tagged redfish at Eastport, Maine (Kelly and Barker, 1961). Redfish from deep water are extremely difficult to tag because they are in such poor condition when brought to the surface owing to the expansion of the swimbladder gases resulting from reduced pressure. Kelly and Barker rediscovered a stock of inshore redfish (first reported by Verrill, 1871) and were able to tag large numbers of these fish after catching them by hook and line near the surface around the docks. He was able to recapture almost all these tagged fish at will and some even as many as 5 or 6 times. The early tagging data indicated an even slower growth-rate than was obtained by otolith studies and thus although the tagging data did not validate the latter, they did favour the slow growth hypothesis. Subsequent data (Kelly and Barker 1963) have shown that after a considerable check in growth

of as much as three years duration after tagging, normal growth was gradually resumed, and this normal growth agreed with the growth rate obtained from ages found from otoliths. Graham (M.S., 1963) reports on these same tagging experiments, and indicates that the substitution of plastic dart tags for the Petersen discs used earlier resulted in no measurable check in growth with tagging and a growth rate which was very close to that obtained from otoliths.

Further evidence supporting the general conclusion of a slow growth rate in Sebastes was reported by Sandeman (1961) for North American mentella-type redfish, for European mentella-type by Surkova (1961), and for Sebastes viviparus by Trout (1961).

Kotthaus, who was present at the meeting, did not make a formal contribution to the discussion of the age and growth problem. The group agreed "That for the study of population dynamics the conception of the slow growth of marinus and mentella, as advocated by a number of the experts, should be accepted" (Rollefsen 1961).

Subsequent to the symposium a few significant papers have appeared, probably the most important of which was that by Surkova (1962). In this paper Surkova shows average length at age values for mentella redfish from several areas of the North Atlantic including divisions of ICNAF Sub areas II and III (Fig 1.1 shows the ICNAF Sub areas as well as other place names and localities mentioned in the text). Zakharov (1962) studied the growth of marinus-type redfish from West Greenland and obtained a growth rate slower than Travin (1959) found for the Barents Sea and Hansen (1961) for the younger fish in the coastal fjords of West Greenland.

Some interesting additional data are provided by Hansen (1963) who reports on his tagging experiments of redfish in Godthåb Fjord*. By 1963 he had obtained 66 recoveries which were usable for providing data on growth, and the table below shows the average growth increments for the periods between tagging and recapture.

Years at large	0	1	2	3	4	5
No of specimens	10	33	12	10	-	1
Increment-limits (cm)	0 - 1	0 - 3	0.5 - 3	0 - 5.2	-	-
Mean Increment	0.6	0.8	1.9	1.1	-	2

Although the sizes of the fish are not given, a slow growth-rate is indicated.

* (A preliminary account of these tagging operations had been presented at the 1959 redfish symposium - Hansen, 1961.)

1.4 Materials and Methods.

This study is based, with the exception of Hermitage Bay where scales were also used, on the examination of otoliths. The validation of the method used to obtain the ages of the fish, and the associated development of the age reading techniques, are to be found in the section concerned with Hermitage Bay. A large part of this section has been taken from Sandeman (1961).

The general localities of the areas where the samples of fish used in this study were obtained, is shown in Fig.1.1. At each of the localities redfish were obtained by otter trawling, the required samples separated from the catch by a sampling procedure and the individual fish examined at sea or in the laboratory to obtain the requisite data. In most cases the following data were obtained from each fish: length, sex, and maturity, and the otoliths were removed for subsequent examination.

All fish lengths reported here are "fork lengths", the measurements being taken from the anterior tip of the lower jaw, with the mouth closed, to the end of the median caudal rays.

For age reading the scales were cleaned in a solution of sodium peroxide and mounted in a gum-arabic solution, on a glass slide, under a coverslip. The winter zones were counted after an image of the scale was projected on to a white surface by a standard scale projector. As only very occasional otoliths were "clear" enough to be read whole, all otoliths were cracked transversely before being examined under a binocular microscope (13x). The cracked surface of the otolith, moistened with 95% ethyl alcohol or immersion oil, was usually viewed by reflected light, with all the otolith surface other than the cracked

surface shielded from the light. For the otoliths of the oldest fish it was usually necessary to use a higher magnification (30x) to distinguish the many fine zones at the outer edge.

Unless stated to the contrary, all age determinations were made by the author.

For most of the data here, Bertalanffy growth curves were fitted to smoothed mean length values at even ages between stated upper and lower limits. These limits were determined by the range of data available for the fit, bearing in mind that the method of Tomlinson and Abramson (1961) requires that there be no gaps in the consecutive ages used, and that the tables only allow a total of 18 groups of ages to be used in the fit. Smoothing was accomplished by use of the formula

$$\bar{l}_t = \tfrac{1}{2} \left(l_{t-1} / 2 + l_t + l_{t+1} / 2 \right)$$

where $\bar{l}_t$ is the smoothed mean length at the even age t and l_t is the observed mean length at the same age. Occasionally, where there were gaps in the unsmoothed data, the formula was suitably modified to provide the requisite interpolation.

Where growth curves are presented in Figures, the thicker line shows the range of ages to which the curve was actually fitted, while the thinner line indicates the extrapolated curve.

2. Hermitage Bay

2.1 Materials and Methods

The fish used in this study were all obtained by otter trawling in Hermitage Bay on the south coast of Newfoundland (Fig. 1.1). This bay is funnel shaped, about 7 miles wide at the mouth with the outer part narrowing down over the course of some 13 miles to a width of 1 mile. From there it continues inland as a narrow cleft, varying in width from 3/4 to 1½ miles before finally terminating a further 11 miles inland. The edges of the bay are steep, and deep water (200 m.) extends over most of the area to very close inshore. Redfish may be caught over the entire deep-water area and, even after the bay narrows to a width of 1 mile, catches of 3,000 - 4,000 pounds (1,360 - 1,820 kg.) per 30-minute haul of redfish have been obtained only 2 miles from the end of the bay.

Hermitage Bay is apparently well suited to redfish, and in the two years before the bay was closed to the larger trawlers (at the Confederation of Newfoundland with Canada in 1949) over 7 million pounds of redfish were taken from the outer part and just outside the bay. There is no shallow bar at the mouth and, although the temperature of the surface and intermediate layers of water are subject to considerable seasonal variation, the temperature of the bottom water, which is likely of Atlantic origin, has remained within rather narrow limits and at depths between 250 and 300 m. has varied only between 4.5° and 6.0°C. during the six years when detailed hydrographic data have been obtained.

The vast majority of the hauls were made in a rather restricted area of about 3 square miles in the depth range 130 - 145 fathoms (238-265 m). A few hauls outside this area, but still within an area of about 14 square miles and in the depth range 120 - 180 fathoms (220 - 330 m), have also been included. The variation in the catches between the extremes of the depth range may be considerable, both in catch per unit effort and in length-frequency distribution, but in this examination of age and growth it is considered that this variation is of little importance.

In the area where most hauls were taken and where the depth range was 130 - 145 fathoms (238 - 265 m), the fish are almost entirely of the typical mentella-type. This is illustrated by the fact that in some 170 hauls made during the year 1958, only 36 marinus-type fish were taken as compared with over 147,000 mentella. In depths at the shallow end of the complete depth range and over a more rocky bottom, marinus were found to be slightly more plentiful, but were still outnumbered by far by the normal typically mentella form. It is thus considered that the rate of growth reported here may be regarded as a preliminary estimate of that of the North American mentella-type redfish.

2.2 Growth-rate of juvenile fishes

2.21 Examination of length-frequencies (Petersen's method)

Hansen (1957, 1958 a, b, and c and 1959) has reported a very interesting series of length measurements of small redfish from Godthåb and Tunugdliarfik Fjords taken during various months of the year from 1952-1957.

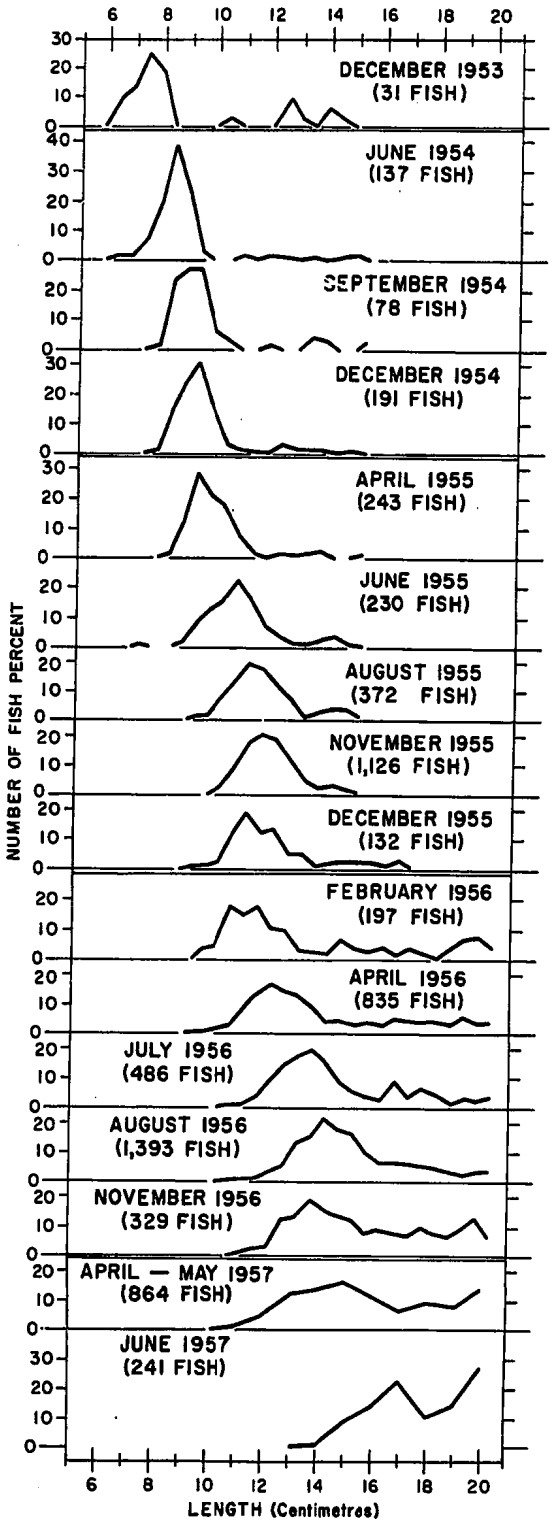

Figure 2.1 Length-frequencies of small redfish (sexes combined), caught in Hermitage Bay, 1953-1957.

These measurements illustrate the progression of the modes of different year-classes, and allow an estimation of the growth-rate during the early years of the fish's life. These data show an extremely slow rate of growth.

A similar series of length measurements of small redfish taken in Hermitage Bay during various months of the year from December 1953 to November 1955 has been reported by Sandeman (1957, 1958), and this series was continued in somewhat less detail during the period 1956-1959 (Sandeman, 1961), and in later years the population has been sampled once per annum.

The small fish were caught by means of a No. 35 or 35A* otter trawl, the cod-end of which was lined or covered with either ½" mesh nylon or 3/8" mesh cotton netting.

During the years 1953, 1954 and 1955, all fish with lengths of 15 cm and under were separated from the catch and measured to the nearest mm.

In Fig 2.1 the measurements have been combined in 0.5 cm groups and the numbers of fish occurring in each 0.5 cm group have been expressed as percentages of the total number of fish 15 cm and under. In 1956 all fish with lengths of 20 cm and under were separated from the catch and measured in 0.5 cm groups. The measurements have been plotted in 0.5 cm groups, and the numbers of fish in each 0.5 cm group have been expressed as percentages of the total number of fish 20 cm and under. In 1957 no special attempt was made to separate the small fish, and they were measured to the nearest centimetre as they occurred in the complete catches or in random samples of the complete catches.

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*The No. 35A otter trawl is a modified No. 35 trawl, but in both nets the width of the mouth of the net is the same, the headline having a length of 50 feet (15.25m).

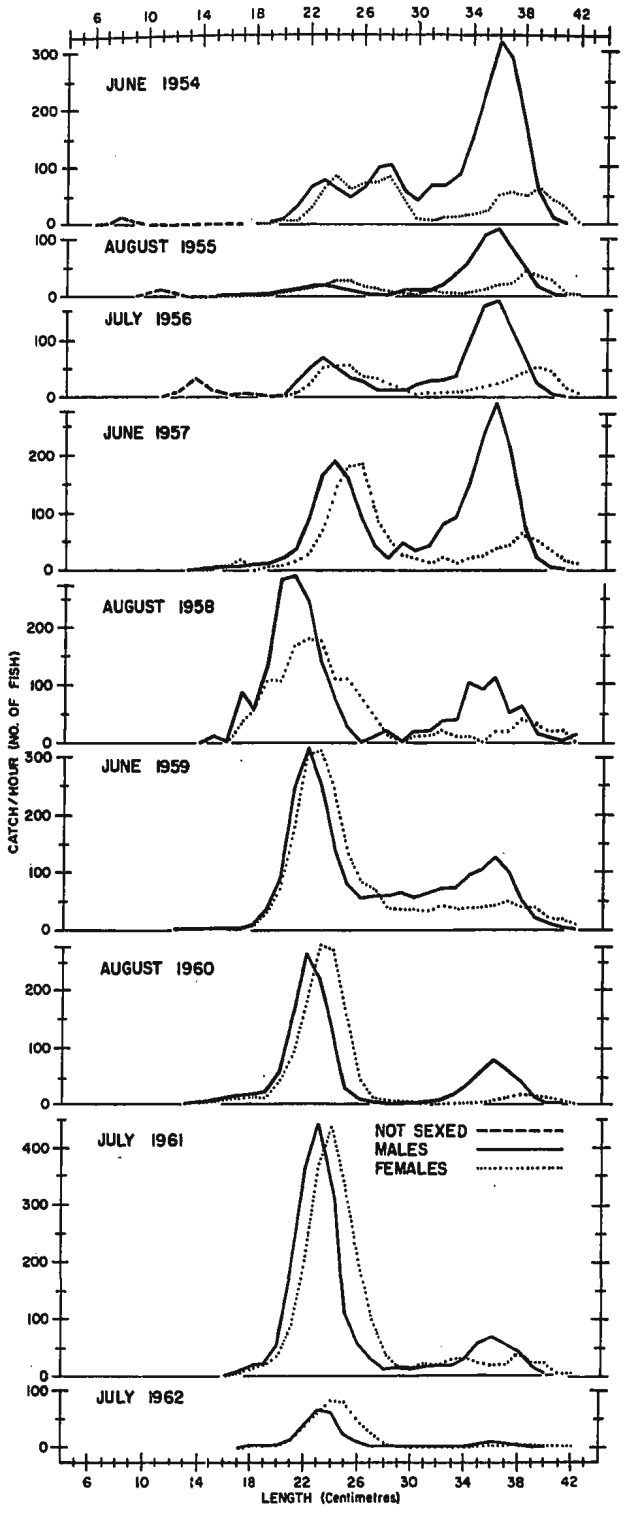

Figure 2.2 Length-frequencies of all redfish caught during trips to Hermitage Bay, 1954 to 1962. (Only sets in which a fine meshed cover was used have been included).

In Fig 2.1 the 1957 data have been plotted in centimetre groups and are expressed as percentages of the total number of fish 20 cm and under.

The progression of the modes from December 1953, through the subsequent months and years to 1956 can clearly be observed in Fig 2.1. This is particularly so, since the dominant group represents a single year-class.

In 1957 this dominant group of small redfish cannot be so easily discerned and by 1958, 1959 and later it had, to a great extent, lost its identity, having started to merge with the peak above it. During these latter years the group can no longer be isolated, and must be examined in relation to the length-frequency of the complete catch.

Fig 2.2 shows the length-frequencies of the complete catch in terms of numbers of fish caught per hour at each centimetre group during selected trips for the years 1954 - 1962. The catch per hour is based on the catches of a No. 35 or No. 35A net having the cod-end covered with ½ inch nylon or 3/8 inch cotton netting. The trips have been selected to be representative of that period of the seasonal cycle when largest catches are to be expected in the area (June to September). The merging of the group of small fish with the peak above it can be observed, and it appears that this group is exerting a considerable influence on the fish which make up this peak.

2.22 Growth-rate from scales and otoliths.

Although many workers have used the otolith or scale methods, or both, for estimating the ages of redfish, few have had good opportunities for checking on the validity of the method used.

Because the divergence of opinion between those who favour a slow growth-rate and those who favour a fast growth-rate is due, most likely, to the different methods of age estimation, the establishment of the validity of the method used becomes of the utmost importance.

Perlmutter and Clarke (1949), after examining the scales of redfish obtained from the Gulf of Maine during various months of the year, have shown that, in a single year, the scales reveal but a single zone of widely spaced circuli followed, during the period November through March, by a zone of closely spaced circuli.

North American biologists have also found that for redfish of the Gulf of Maine (Anon, 1957; Kelly and Wolf, 1959) growth of the otoliths shows but a single pair of opaque and hyaline zones to be formed during a single year.

Bratberg (1956) has shown, by examination of the otoliths from samples taken from a stock of juvenile fish at various intervals throughout a period of over a year, that one opaque and one hyaline zone constitute an annual ring, and that the edges of the scales were found to correspond to this, a single band of broadly spaced circuli followed by a single band of narrowly spaced circuli making the scale growth for a single year.

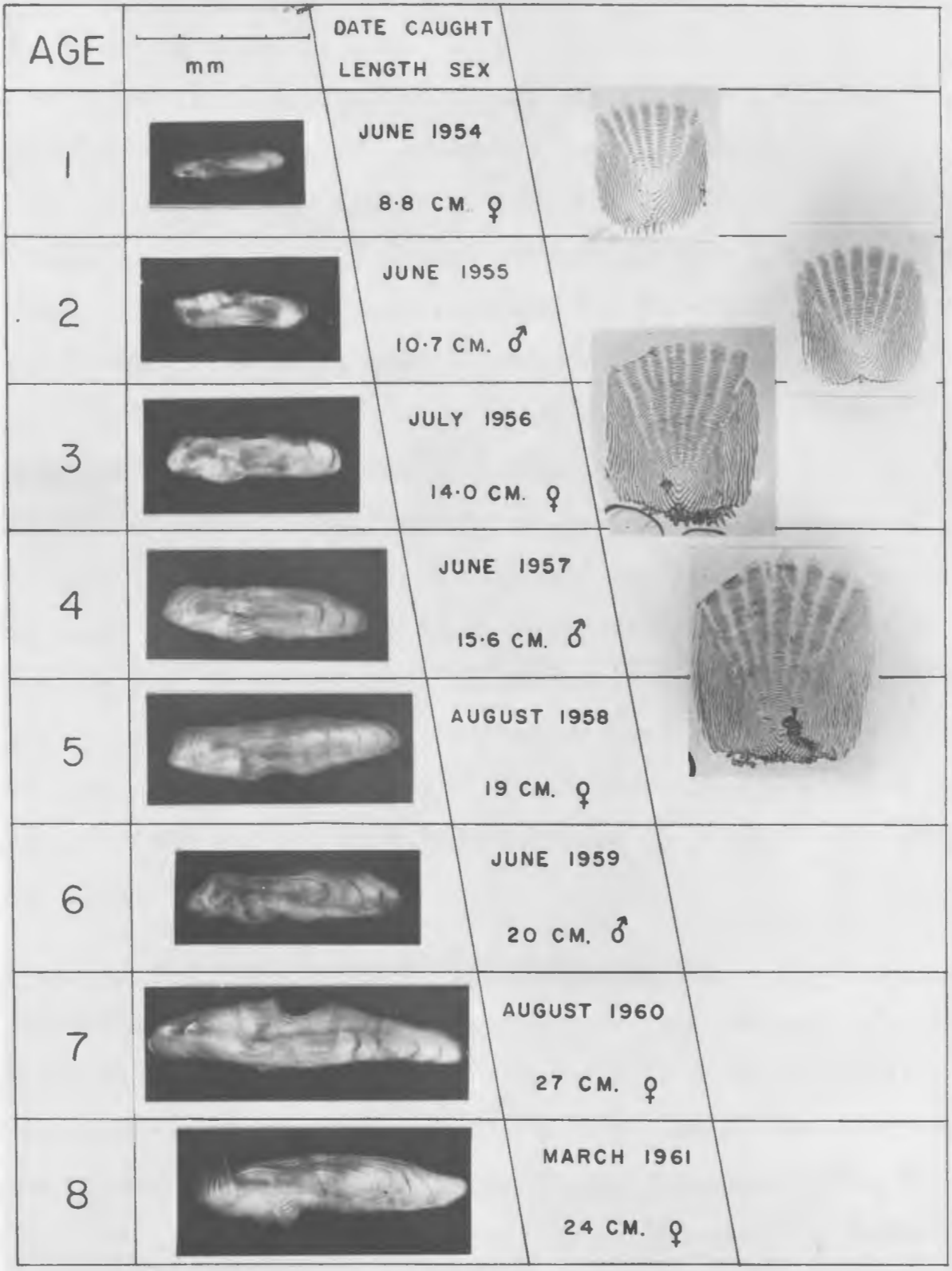

FIGURE 2.3 SELECTION OF BETTER OTOLITHS TAKEN FROM REDFISH OF THE DOMINANT 1953 YEAR-CLASS IN THE SUMMER OF EACH YEAR, 1954 TO 1961. EACH OTOLITH HAS BEEN CRACKED TRANSVERSELY AND THE CROSS-SECTION IS VIEWED HERE IN REFLECTED LIGHT. SCALES ARE ALSO SHOWN FOR THE SAME FISH FOR THE YEARS 1954 TO 1957.

The group of small redfish, which has been followed for a number of years in Hermitage Bay, Newfoundland (Fig 2.1), has also revealed that during a single year scale growth shows only the formation of a single band of widely spaced circuli followed by a single zone of narrowly spaced circuli (Sandeman, 1958; 1961). This group of fish has now been followed for 10 years, and although it becomes rather difficult to distinguish between the zones of the scales after the fish are about 4 years old, the otoliths have remained relatively clear, and in each successive year a further pair of zones, a hyaline and an opaque, can be observed to have been laid down.* The duration of the period in which the different zones are formed is somewhat variable, apparently depending on the characteristics of the water and food during the different years, but in general the opaque zone of an otolith is laid down between April - May - June to September - October - November, and the hyaline zone from September - October - November to about April - May - June.

2.23 Ages of the small redfish from Hermitage Bay

The small redfish in Hermitage Bay first appear on the bottom during the winter months when they are about 60-80 mm in length. It is perhaps worthy of comment that at this time of the year the water column above is almost uniform in temperature from top to bottom, and the characteristic cold water intermediate layer (-1.0° to $1.0^{\circ}C$), which throughout the remainder of the year is always present to a greater or lesser extent, has been dissipated.

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*Fig 2.3 shows a selection of better otoliths taken from redfish of this dominant year-class in the summer of each year 1954 to 1961. Scales are shown from the same fish for the years 1954 to 1957.

During the winter in which they first make their appearance on the bottom, the first indications of a definite hyaline zone of the otolith and the first zone of narrowly spaced circuli on the scales may be observed. It is not, however, known for certain whether or not this 1st zone of narrowly spaced circuli of the scales and the first definite and clear hyaline zone of the otoliths really represents the first "winter" of the fish, and whether the extensive growth from about 7 mm in May - June, when the larvae are extruded, to 60-80 mm in December takes place during the first year of life of the fish, or whether the pelagic period of its post-larval life extends over a period greater than a year.

Whether the fish are in their first year of life or older at the time of formation of the 1st hyaline zone of the otoliths or 1st zone of narrowly spaced circuli of the scales does not affect the use of otoliths and scales for the determination of age, and provided the age determination is consistently referred to the easily distinguishable 1st definite hyaline zone of the otolith and the equivalent first zone of narrowly spaced circuli of the scales, the determination of age from otoliths and scales may proceed.

All the ages used in this paper are referred to the 1st definite hyaline zone of the otoliths and the corresponding 1st zone of narrowly spaced circuli of the scales as being the 1st "winter" zone of the fish's life. Thus a fish caught in December having scales showing only widely spaced circuli with no zone of narrowly spaced circuli, and otoliths with only an opaque zone would be considered as in their first year of life or Age 0.

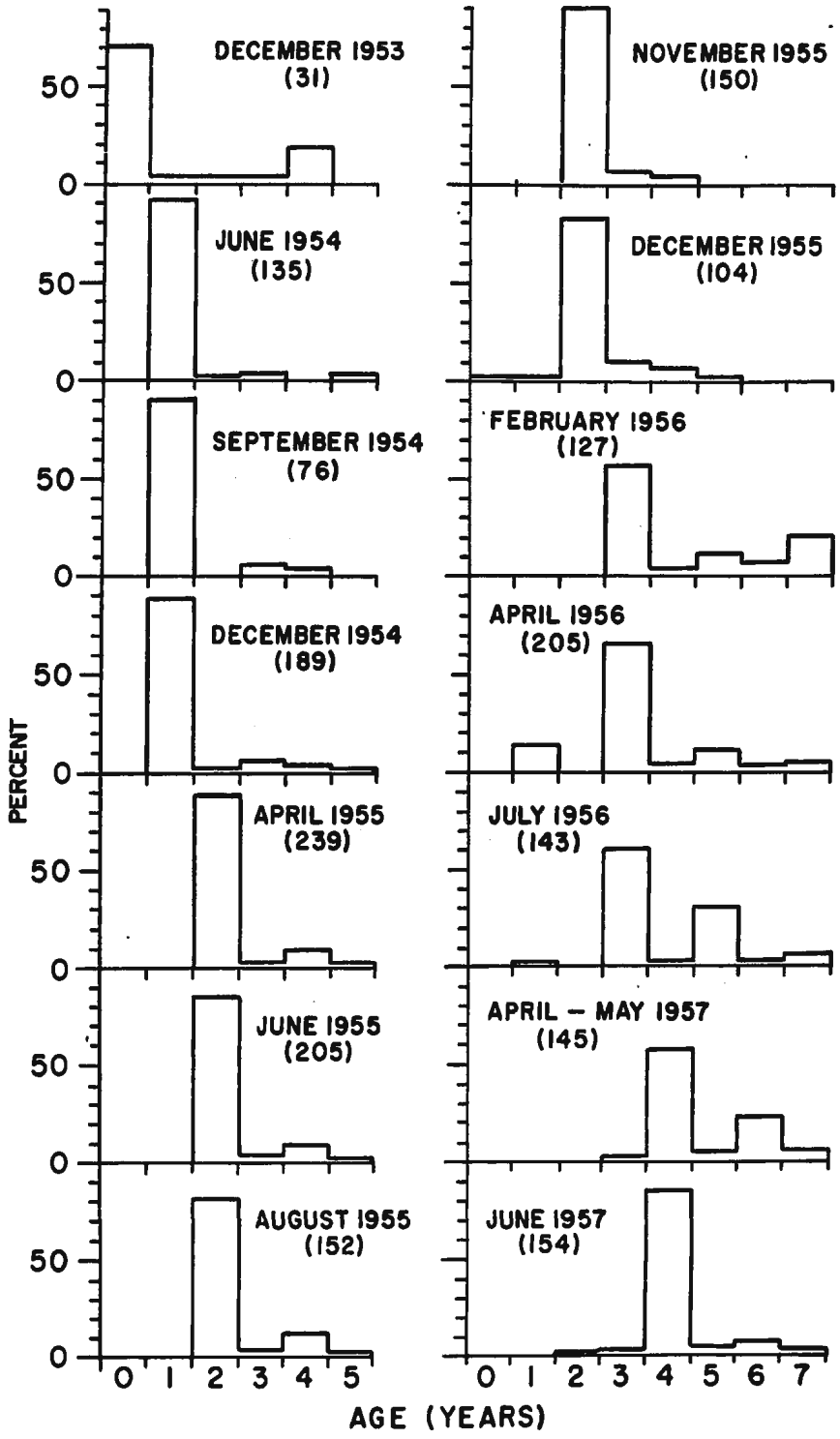

Figure 2.4 Age-frequencies corresponding to the length-frequencies shown in Fig. 2.1. The numerals in parenthesis indicate the numbers of fish, the otoliths of which were examined for age determination.

The end of each zone of "winter" growth is coincident with the "birth date" of the fishes and thus a straight count of the number of complete "winter" zones provides the estimate of age. Because so little growth takes place during the months January to May, it is convenient to regard the birth date as in the previous January so as to put the estimated ages on a calendar year basis.

In the years 1953-1957, random samples, usually of about 150 fish, were obtained from the small redfish caught during each trip to Hermitage Bay. These fish were usually measured to the nearest millimetre before being preserved in 95% ethyl alcohol for later examination at the laboratory. The scales and otoliths were subsequently removed and preserved in vials containing 95% ethyl alcohol.

For the younger fish (to about 4 years of age) the otoliths and scales were read independently, and the few age estimations which did not agree were re-read and argued to best agreement. In the older fish of the series no recourse was made to the scales, and two independent age estimations from the otoliths served the same function.

Age-frequencies, corresponding to the length-frequencies in Fig. 2.1 are shown in Fig. 2.4. These have been expressed as percentages of the fish, 15 cm and under, occurring in the sample during 1953, 1954 and 1958, and percentages of the fish 20 cm and under, during 1956 and 1957.

These age-frequencies emphasize the fact that the group of small fish is made up of a single year-class which, for several years, dominates the year-classes both above and below it, and that, during the four years following the settlement of this dominant

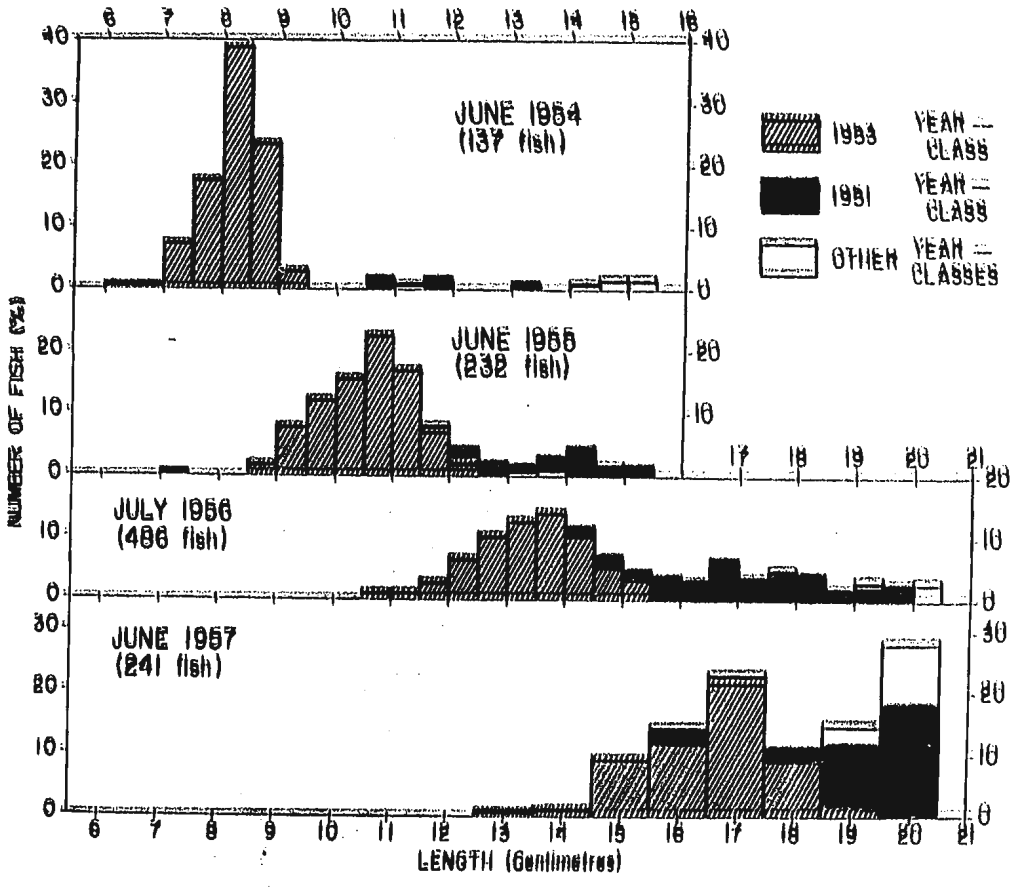

Figure 2.5 Length-frequencies shown in Fig. 2.1 for June or July, 1954 to 1957, broken down to show the year-class composition at each length group.

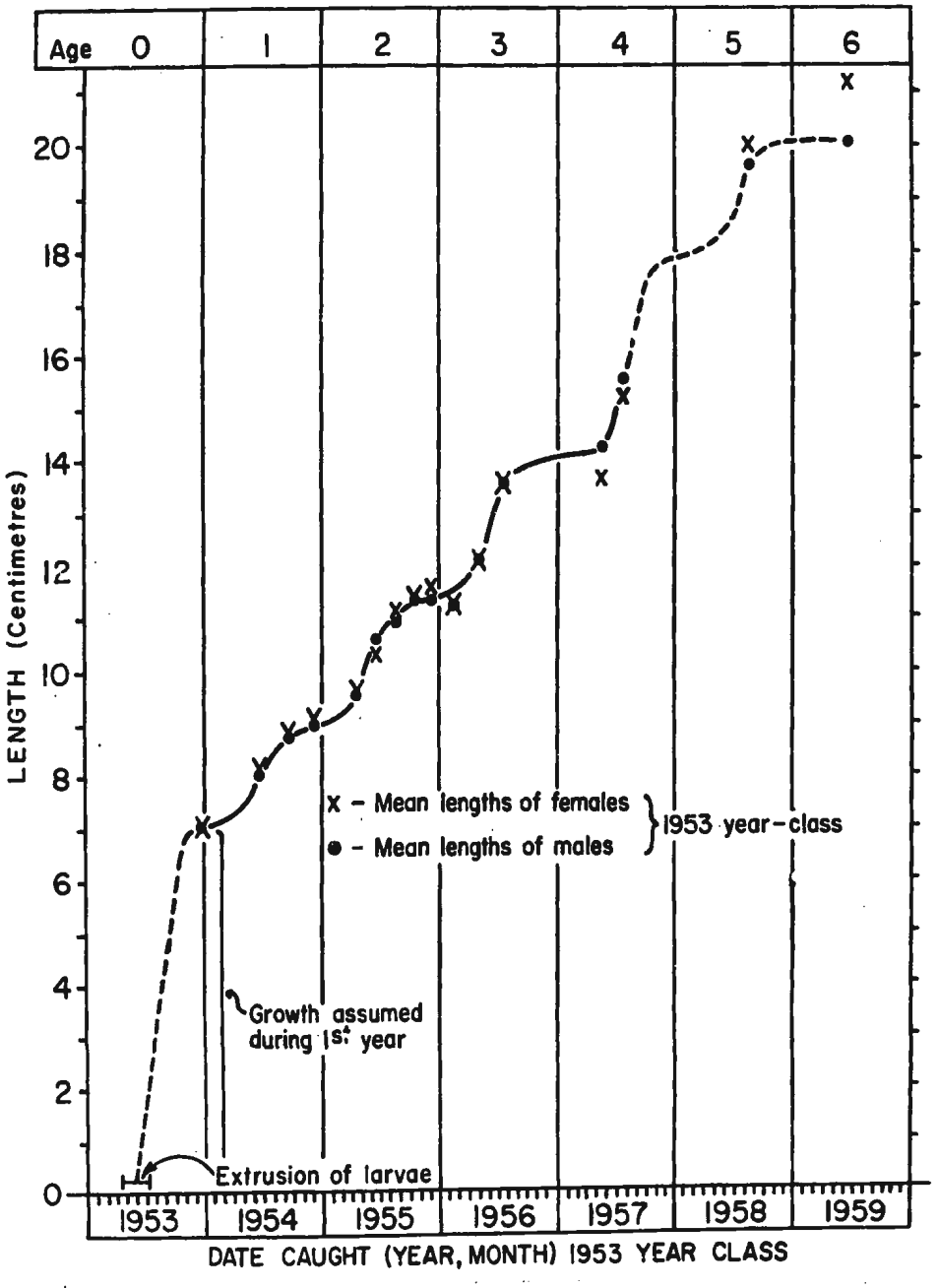

Figure 2.6 Growth of the group of young fish (1953 year-class) in Hermitage Bay, as shown by the mean length of the year-class at the time of catching. Only the curve for the males has been drawn.

year-class, only very few fish of more recent year-classes have succeeded in settling to the bottom in this area.

The dominance of the 1953 year-class can be more clearly seen in Fig. 2.5 where the length-frequencies shown in Fig. 2.1 for June or July 1954-1957, have been broken down to show year-class composition at each length group. The length-frequencies are presented as histograms and, for the sake of clarity, only the 1951 and 1953 year-classes are shown separately, all other year-classes being combined together. The cominance of the 1953 year-class is quite striking. The mean lengths of the fish of this dominant year-class have been calculated at each time of sampling, and Fig. 2.6 indicates the rate of growth of this single year-class during the period 1953 to 1959. The mean lengths of the fish of this dominant year-class were calculated for most samples from measurements made before preservation in ethyl alcohol. For a few samples, only measurements made after preservation were available, and in these cases the mean lengths of fish after preservation have been converted to mean lengths of fish when fresh. During 1954, 1955 and 1956 sufficient samples were obtained at different seasons of the year to illustrate the seasonal growth cycle, but in the more recent years adequate sampling of the year-class by nets with fine meshed covers has been restricted to but one or two trips, and the seasonal cycle cannot be recognized.

Fig. 2.7(a) shows the growth curves for these same fish, but here the data for the years 1960 and 1961 has been added and only one mean length is shown for each year, this being chosen from the nearest sample to June 30th.

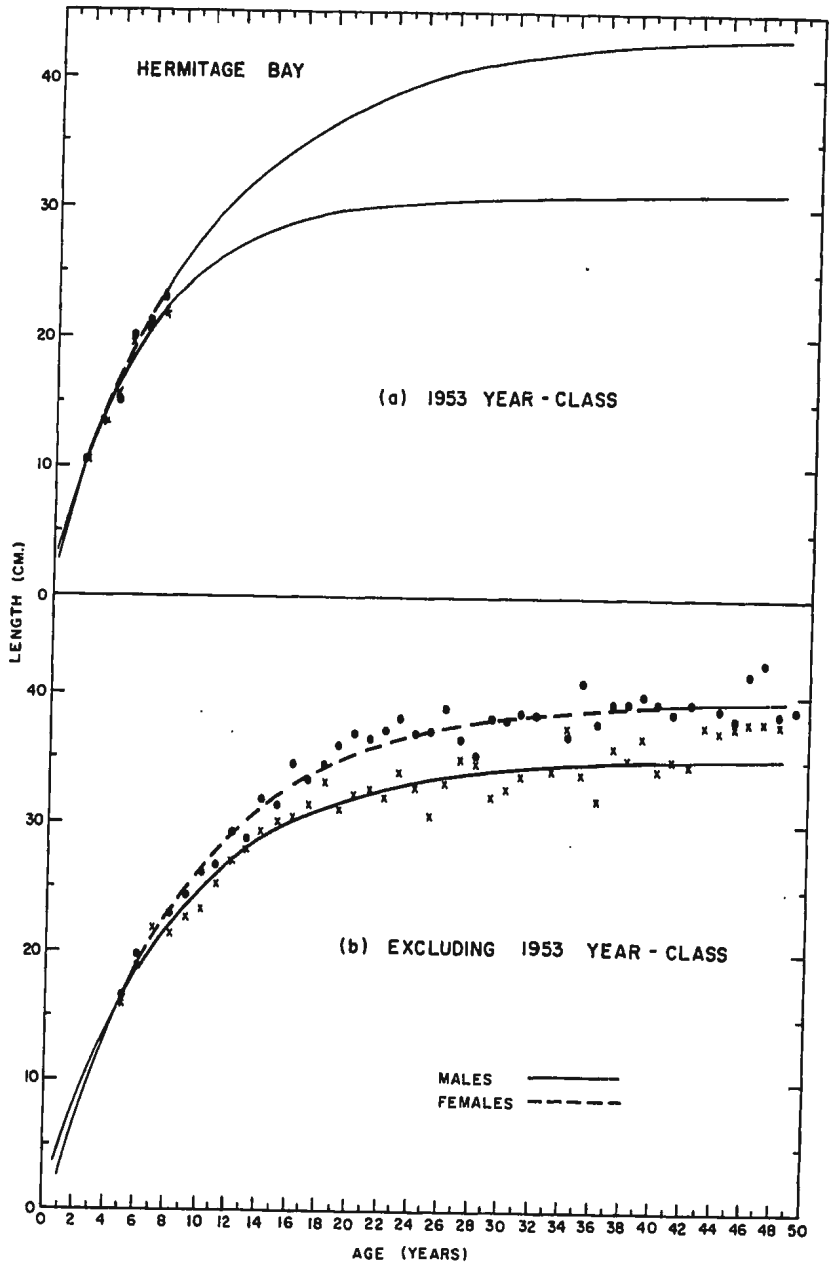

FIGURE 2.7 GROWTH CURVES OF KENTELLA FROM HERMITAGE BAY

(a) 1953 YEAR-CLASS

(b) LARGER FISH EXCLUDING THE 1953 YEAR-CLASS.

IN THIS AND THE FOLLOWING FIGURES SHOWING GROWTH CURVES AND THEIR DERIVATIVES, THE THICKER LINE SHOWS THE RANGE OF AGES TO WHICH THE CURVE WAS ACTUALLY FITTED WHILE THE THINNER LINE INDICATES THE EXTRAPOLATED CURVE.

The curves in this figure are those of the Bertalanffy growth equation fitted to the mean lengths of ages 2 to 7 by the method of Tomlinson and Abramson (1961).

The Bertalanffy growth equations are as follows:-

$$\text{Males.} \qquad l_t = 31 \left\{ 1 - e^{-.17\ (t + .4)} \right\}$$

$$\text{Females.} \qquad l_t = 43 \left\{ 1 - e^{-.10\ (t + .7)} \right\}$$

Because the curves have been fitted to the length data for so few and such young age groups, the parameters are rather meaningless and this is shown up when the constants of the Bertalanffy equations are examined in conjunction with their 95% confidence limits.

Parameter	Males	Females
L_{oo}	31 ± 28	43 ± 95
K	0.17 ± 0.35	0.10 ± 0.37
t_o	-0.4 ± 1.6	-0.7 ± 1.7

Considering the very high standard errors involved, it is remarkable how well the curve of best fit for these young fish agrees with the curves for the older fish which are derived later.

2.3 Growth of the larger fish

2.31 Examination of length-frequencies

The length-frequency distribution of the fish in Hermitage Bay, as observed during the years 1953-1959, is characteristically tri-modal (Fig 2.2). In addition to the group of young fish, tentatively regarded as the 1953 year-class, a second group, having a mode at 22-23 cm for males and 24-26 cm for females, has shown up consistently during the years 1954-1957. The other peak, which for males is well defined at 36cm, is not so clear for the females but it can usually be recognized at 38-40 cm. A further peak, intermediate in position to the two already mentioned occurs occasionally. (It may be seen in the length-frequencies shown for 1954 in Fig. 2.2) The sporadic occurrence of this peak continues to be perplexing, particularly as its appearance and disappearance may occur over a very short period of time.

It has been shown that, for the juvenile fish, the progression of the modes of the length-frequencies, although rather slow, is easily discernible, particularly when consecutive years are considered. An examination of the length-frequencies for all sizes of fish in the catch (Fig. 2.2) does not reveal any easily discernible progression of the two major peaks of the large fish during the nine years for which data are shown. Some progression can be seen in the lower of these two peaks (males at 22-23 cm and females at 24-26 cm) during the years 1954-1957, but in 1958 and later this progression is disturbed by the merging of the 1953 year-class with this group. The peak for large males, which is particularly well defined, remained at 36 cm for the 9 years

shown, and indeed also appeared at the same length group during catches in 1947 and 1948. The corresponding peak for females, although not so clear, also appears to have remained stationary for many years.

The very slight progression of the peak with modal lengths of 22-23 cm for males and 24-26 cm for females and the complete lack of movement of the peak for the large fish are suggestive of a very slow growth-rate, with the oldest fish attaining a final size after which no further measurable growth in length ensues. The relative immobility of the latter peak is interpreted as due to the combined effect of the practically negligible growth that would occur in the fish of considerable age, and the piling up of a large number of year-classes within the single peak.

2.32 Age estimation and growth-curves from otoliths

Although during the early part of the fish's life there is considerable evidence that the annual pattern of otolith growth consists of the formation of a single pair of zones (one hyaline and one opaque), this definite evidence is lacking for the older fish. To extrapolate this principle to fish which are older, and in most cases sexually mature, is perhaps to invite criticism, but in the apparent absence of any real evidence of "split rings" (Graham et al 1954, Trout 1954, 1958) or spawning zones (Rollefsen 1933 and 1935), and failing any other method of obtaining consistency of reading, each hyaline zone, which may be traced along the shorter axis when the cross section of the otolith is examined, has been regarded as representing a further year of life.

Checks or false hyaline zones do occur and may often be seen in the otoliths of the small fish of the 1953 year-class. In following this year-class, it has been noted that it is only the true hyaline zones which may be traced along the short axis, and that the false hyaline zones or checks, when traced round to the short axis, disappear or combine with the true hyaline zone. This can also be seen in the photographs of the otoliths of both Sebastes marinus and Sebastes viviparus shown by Rasmussen (1958).

Ages have been estimated from samples of otoliths obtained from Hermitage Bay during trips in 1953, 1957, 1958 and 1959. Although these samples were obtained in different months and years, it is convenient, because of the large variety in ages occurring and the necessity of separating the males and females, to combine the samples in order to provide even an approach to an adequate total sample. Age estimations have been made from the otoliths of a total of 903 fish, of which 205 fish were of the 1953 year-class. As this year-class appears to have shown abnormally fast growth during the first 4 years, and its numbers are so great relative to the other fish, these fish have been excluded in deriving the mean growth curves shown in Fig. 2.7(b). Thus these curves are based on age estimations from the otoliths of 366 males and 332 females.

The curves shown in Fig. 2.7(b) are Bertalanffy growth curves fitted to the smoothed mean length values for even ages, for ages 6 to 40. The parameters of these curves together with their 95% confidence limits are shown below.

Parameter	Males	Females
L_{oo}	35.2 ± 1.0	39.7 ± 0.9
K	0.119 ± 0.028	0.113 ± 0.019
t_o	-0.3 ± 1.6	0.3 ± 1.0

It is evident from these figures above that we have extremely good estimates of the Bertalanffy parameters. The very low standard error for L_{oo} reflects the fact that we have data extending to the region of the asymptote and are not forced to extrapolate well beyond the range of the data to obtain an estimate for this parameter.

As pointed out already the resemblance between the fitted curves for the larger and older fish and those derived from the mean lengths at age for the 1953 year-class, which we have followed year by year and thus can age them accurately, is very close. This resmeblance suggests some measure of confidence in the method of age determination and the age estimates obtained by it as applied to the older fish of the population.

3. Southwest slope of the Grand Bank

3.1 Material and methods

The Fisheries Research Board of Canada research vessel Investigator II devoted considerable time in 1947 to exploratory fishing in the area of the southwest slope of the Grand Bank, and in the course of 8 trips to the area a total of some 450 fish were brought back to the laboratory for examination. Most of the fishing, however, took place in shallow water (for redfish) and the greatest depth fished was 115 fathoms. Although we have later data for the area, the data presented here is for 1947 only. It was hoped that this data might yield information on the natural mortality rate, for prior to 1947 less than 500 metric tons of redfish was landed from ICNAF Sub area 3 (Templeman, 1959).

It is unfortunate that the data from such a wide area, and from so many sets, must be combined to provide an adequate sample for ageing, but as the depth range is not very great any deleterious effect is unlikely to be of importance. The locations of the different samples and numbers of fish yielding otoliths for study are indicated in Fig. 3.1.

Although the samples were not examined for the presence of marinus, it is most unlikely, from our subsequent knowledge of the numbers of these fish in the area, that more than the occasional marinus fish was caught. The growth curves presented here can thus be considered as those of North American mentella-type redfish.

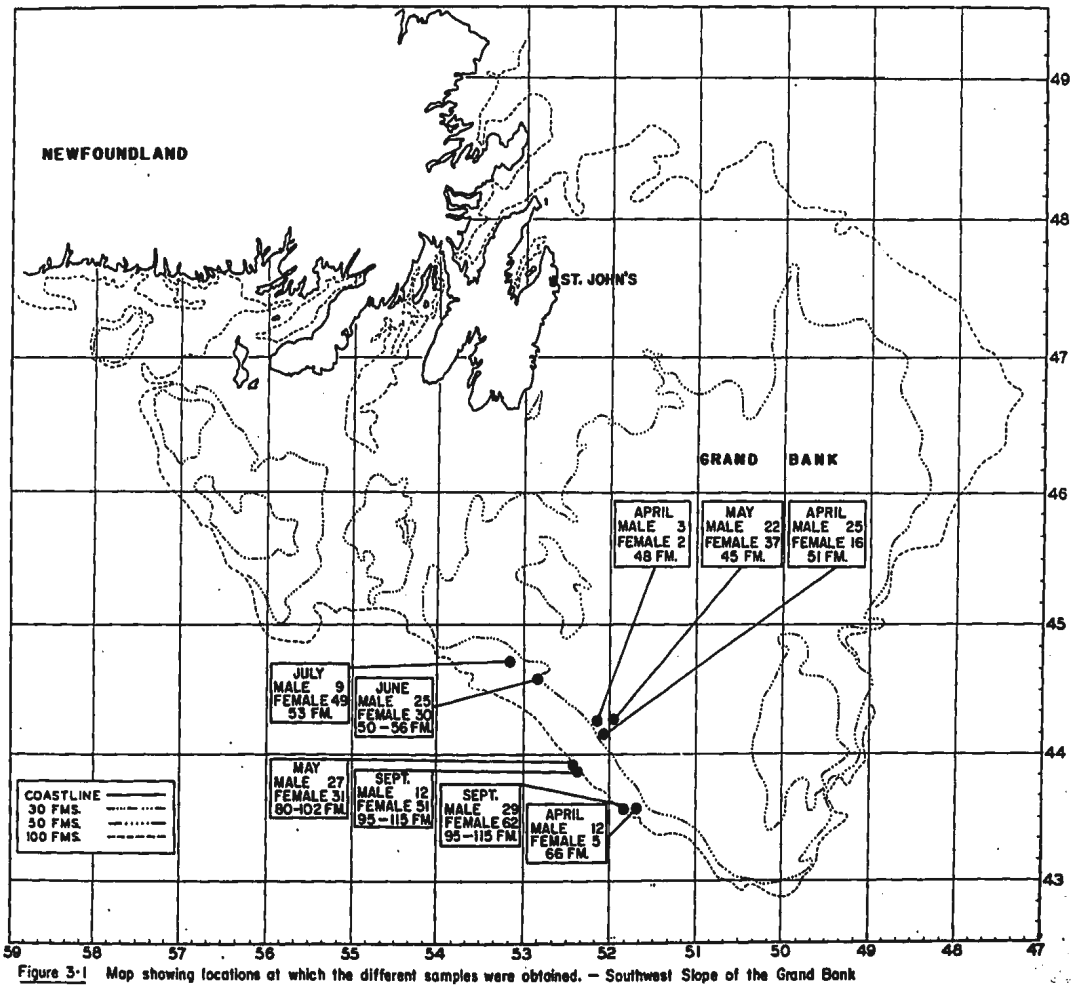

Figure 3-1 Map showing locations at which the different samples were obtained. — Southwest Slope of the Grand Bank

3.2 Comparison of ages and growth-rates as determined by two different persons.

The otoliths from the southwest slope of the Grand Bank have been examined and ages estimated by two different persons, the author and technicain E. E. Squires. This provides an opportunity to examine the variation occurring between the two age readers who are attempting to determine the ages, using exactly the same basic method. It is not very frequently when ages are estimated from redfish of 10 years old or older, that two age readers will obtain the same age reading and indeed, in this comparison, out of a total of 444 ages only in 43 cases was complete agreement obtained.

Fig. 3.2 shows the number of times in which agreement or disagreement occurred between the two age readers, Squires and Sandeman. It is evident from this figure that there is a wide variation between the ages as determined by these readers. Furthermore, the spread of the data on the upper side of the diagonal of complete agreement indicates that the ages estimated by Squires are on the average, higher than those estimated by Sandeman. This may perhaps be better seen by examining the frequency of agreement and disagreement without reference to the actual ages at which the agreements and disagreements occurred. This has been done in Fig. 3.3, which may be considered as a "difference frequency histogram". The shape of this histogram approximates to a normal curve and thus indicates a rather large random error but also, because the curve is skewed to the right, it indicates that Squires on the average obtains age estimates

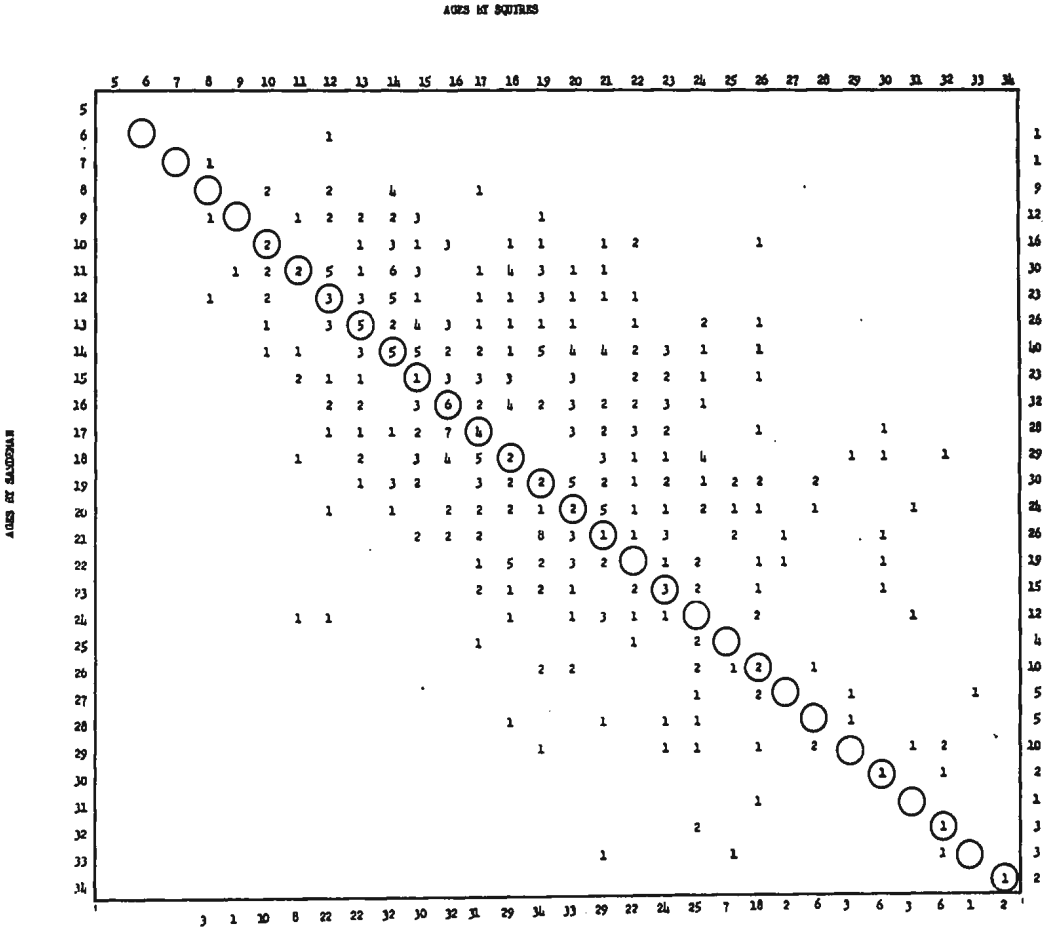

FIGURE 3.2. DIAGRAM SHOWING FREQUENCY OF AGREEMENT AND DISAGREEMENT IN AGE ESTIMATES FROM THE SAME FISH BY TWO PERSONS. THE BOXED DIAGONAL DENOTES THE FREQUENCY OF PERFECT AGREEMENT AT EACH AGE. A TOTAL OF 5 FISH OLDER THAN AGE 34 HAVE BEEN OMITTED FROM THE TABLE, ALTHOUGH THEY ARE INCLUDED IN THE TOTALS FOR EACH AGE.

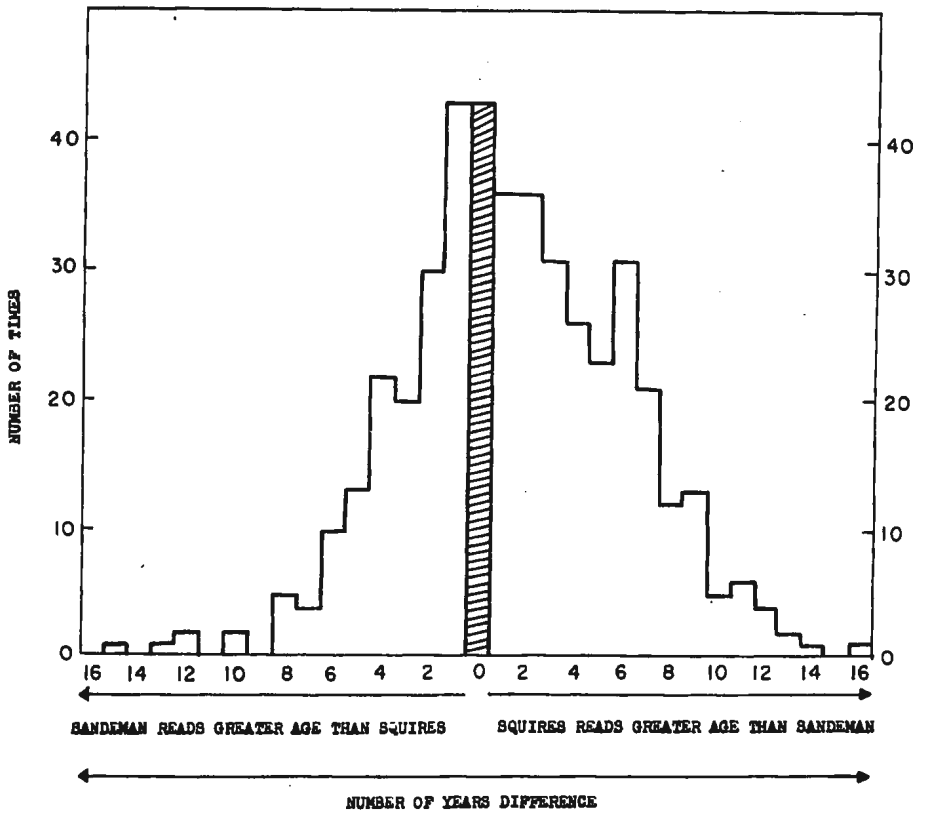

FIGURE 3.3 AGREEMENT-DISAGREEMENT FREQUENCY HISTOGRAM. COMPARISON OF OTOLITH AGE ESTIMATES OF THE SAME FISH BY TWO DIFFERENT PERSONS, E.J.SANDEMAN AND E.E.SQUIRES.

that are slightly higher than those of Sandeman.

We would infer from the rather poor agreement between the two age readers (about 10% agreement) that, particularly when the older fish are considered, investigations involving year-classes and comparisons of their relative abundance will be rather abortive, unless very large numbers of otoliths are examined. This however does not concern us here, for apart from the especially abundant year-classes of young fish, which can be recognised by their size and abundance alone without recourse to otoliths, we are not dealing with year-classes but with overall growth curves. We should examine, however, how the agreements and disagreements referred to above affect the growth curves and equations of growth that are derived from them.

The values for mean length at each age, as calculated from the age estimations of Squires and Sandeman for males and females separately, are shown in Fig. 3.4. Also shown are the least squares Bertalanffy curves fitted to the smoothed mean length at age data for ages 8 - 34 (because of the lack of data at age 33, 34 and 35 for females in Sandeman's data, this curve was fitted to the smoothed data for ages 8-32). The curves derived from the two different persons appear so similar in this figure that it is difficult to see any difference at all. To see any difference, it is really necessary to plot the curves as derived from the data of each age reader on the same co-ordinate system, and this has been done in Fig. 3.5. It is apparent in this figure that the agreement for males is indeed very close, and that from ages of about 8 to 24, the curves as derived from the data of Squires and Sandeman are virtually coincident. The comparison between the two curves for the females confirms that which was indicated in

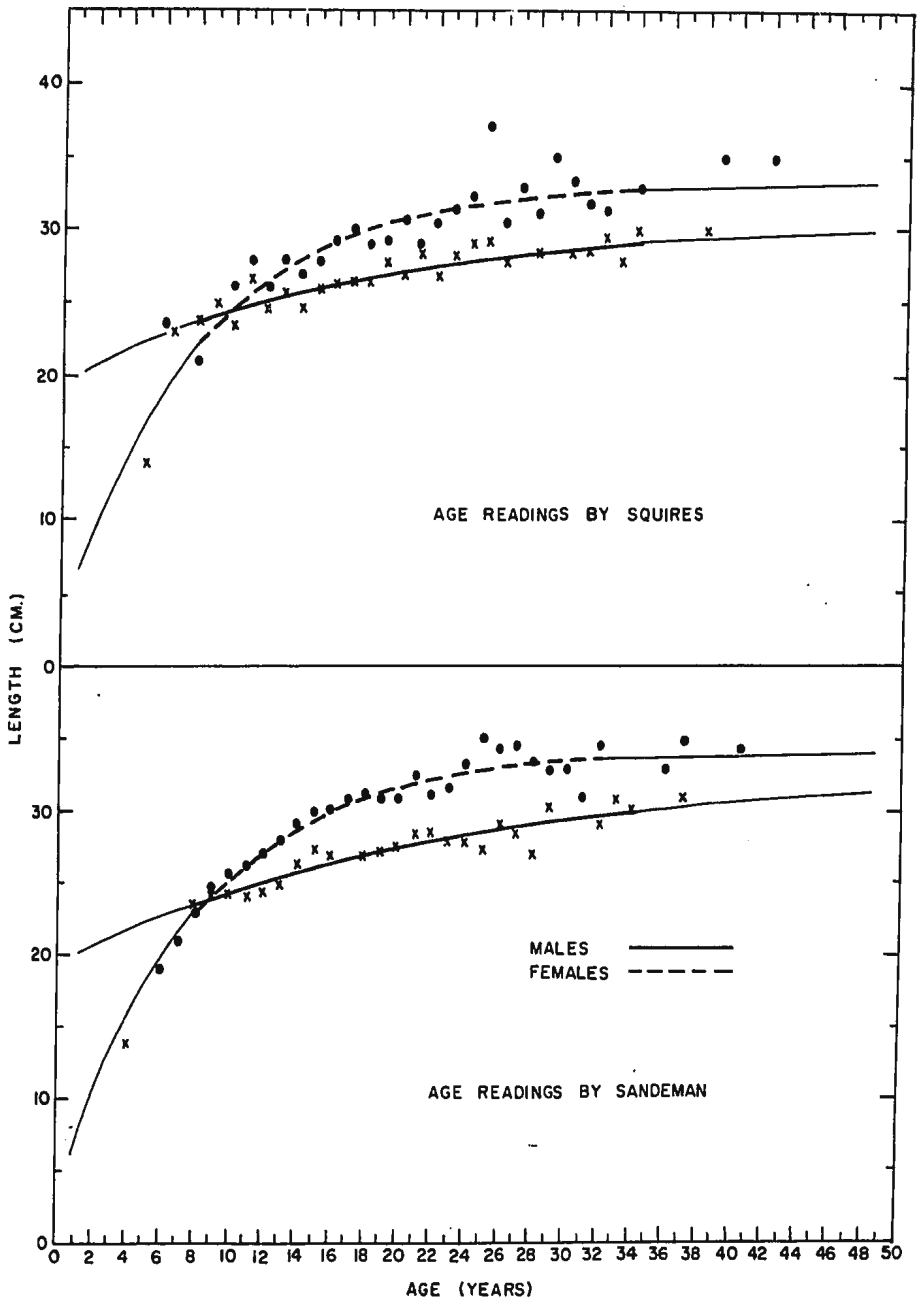

FIGURE 3.4 GROWTH CURVES OF MENTELLA REDFISH FROM OTOLITH AGE ESTIMATES OF TWO PERSONS - SOUTHWEST GRAND BANK.

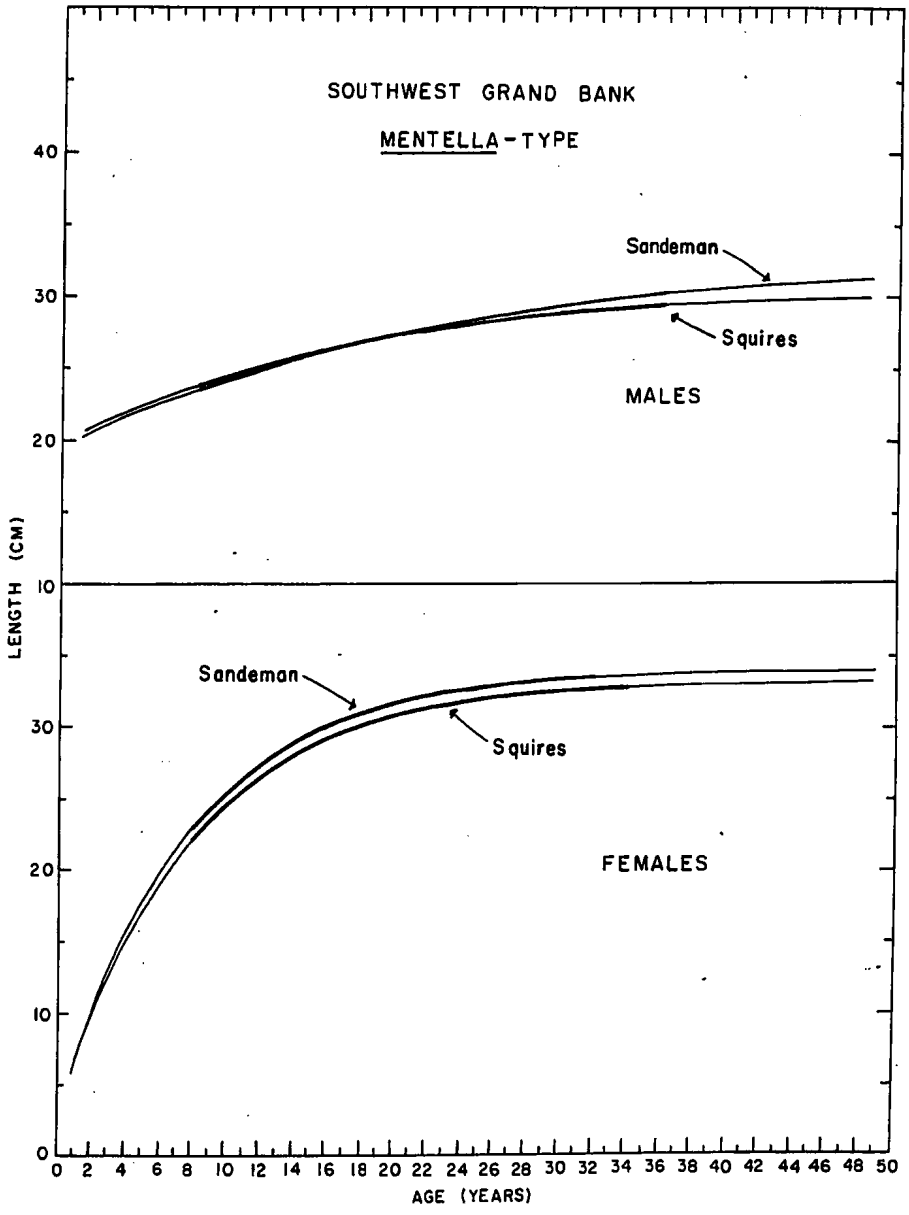

FIGURE 3.5 GROWTH CURVES OF MENTELLA REDFISH FROM OTOLITH AGE ESTIMATES BY TWO PERSONS -- SOUTHWEST SLOPE OF THE GRAND BANK.

Fig. 3.2 and 3.3, namely that Squires tended to read the ages slightly higher than Sandeman, and this is reflected in the curve from the latter's data being slightly above that of the former.

The agreement between the two curves for the male fish is all the more striking because we have what might seem to be a highly abnormal curve. A glance at the Bertalanffy equations for these curves will show that we have the astonishing values of - 17 and - 20 for the parameter t_o, and when the curves are extrapolated beyond their fitted range we find that the males would be 20 cm in length when born. This illustrates the danger of extrapolation beyond the range of the data, a danger, which because of our lack of data on small fish, affects our estimates, particularily of t_o, but which for most species of fish affects, that in many ways more important parameter, L_{oo}.

The parameters of the Bertalanffy equations and their standard errors are tabulated below.

Parameter	Males		Females	
	Squires	Sandeman	Squires	Sandeman
L_{oo}	30.6 ± 2.3	33 ± 6	33.3 ± 2.0	34.2 ± 1.4
K	0.06 ± 0.04	0.05 ± 0.05	0.13 ± 0.07	0.13 ± 0.05
t_o	- 17 ± 5	- 20 ± 6	- 0.7 ± 4.5	- 0.7 ± 3.0

It is evident from the considerable overlap in the confidence limits of all the parameters above that, for both males and females, the growth curves derived from the age estimates of Squires and Sandeman can be considered similar.

This is a very useful result for it means, providing it is growth curves and the equations of these curves in which we are interested and providing neither person deviates from the basic method of age determination, that otoliths read by either Squires or Sandeman may be used for the derivation of growth curves and the equations thereof, and that these curves and equations can be directly compared.

3.3 Growth curves of mentella redfish

The growth curves and fitted equations are discussed in section 3.2.

4. Gulf of St. Lawrence.

4.1 Introduction.

In the Gulf of St. Lawrence, the history of the redfish stocks and the effect of the fishery on these has been of very great interest. The fishery, which only started in the early 1950's, rose rapidly to a peak in 1955, when landings of almost 50,000 metric tons were recorded. In subsequent years the landings have decreased, till in 1962, the most recent year for which figures are available, only 6,500 metric tons were landed from the area. The St. John's Biological Station has followed this brief history of exploitation with considerable interest.

Although most of the likely redfish areas in the Gulf of St. Lawrence had been examined by the Investigator II during 1947 and 1948, it was not till 1950 that a fine-meshed liner was used inside the codend of the No. 36 otter trawl net used by this vessel. In 1953 a regular pattern of fishing stations was established in the area, and since this time most of the fishing stations have been visited every second year. With the coming of the A. T. Cameron in 1958, the regular Gulf of St. Lawrence redfish survey trips have been made by this ship, and the larger No. 41.5 otter trawl with a lining of 1 1/8" nylon has been used.

The regular pattern of fishing stations consists of six major fishing areas (Fig 4.1), and at each area an attempt is made to fish a series of standard depths. In the Gulf of St. Lawrence where the maximum depth is limited to about 250 fathoms and where, presumably because of the muddy nature of the bottom in the centre of the channels, very few redfish occur below 200 fathoms, the

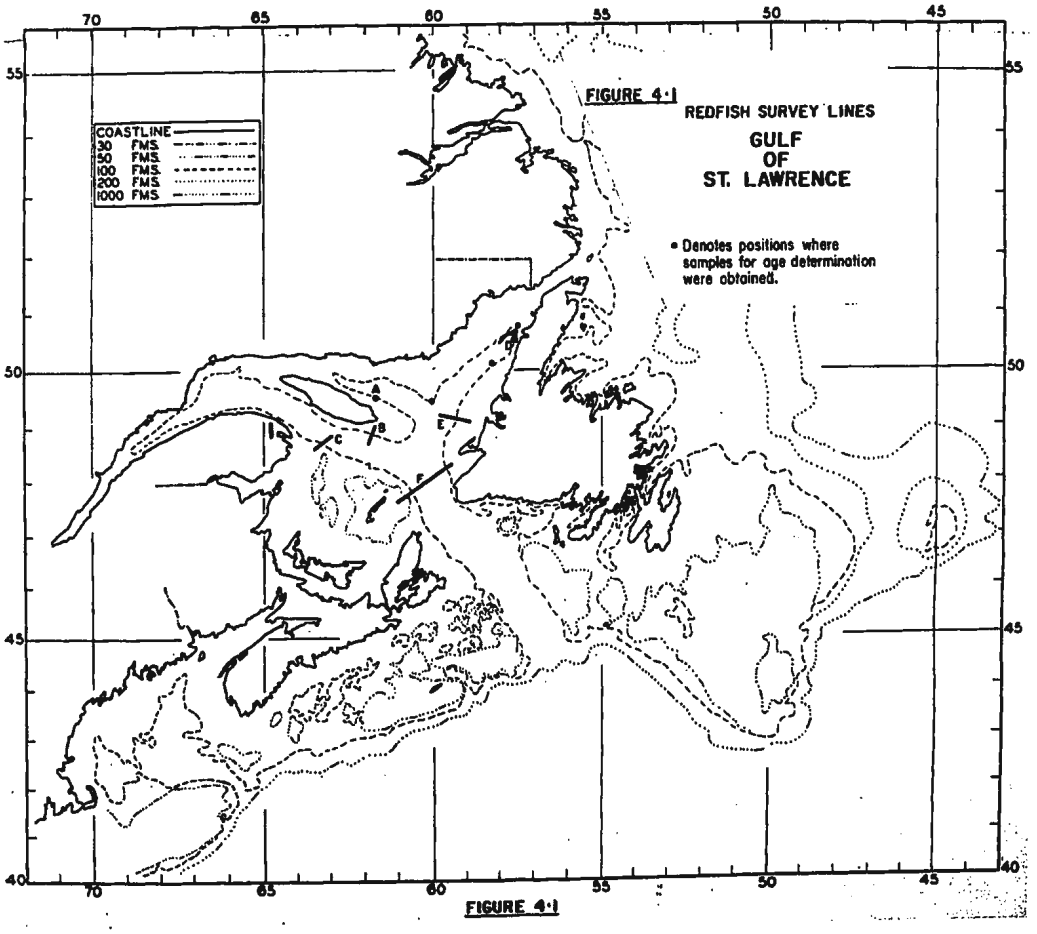
70
65
60
55
50
45
55
50
45
40
COASTLINE
30 FMS.
50 FMS.
100 FMS.
200 FMS.
1000 FMS.
FIGURE 4·1
REDFISH SURVEY LINES
GULF
OF
ST. LAWRENCE
• Denotes positions where samples for age determination were obtained.

FIGURE 4·1

depths fished in each area were usually 100, 120, 140, 160 and 180 fathoms.

4.2 Growth by Petersen's method

Fig. 4.2 shows length-frequencies for redfish from an area in the Esquiman Channel (Fig. 1.1). These fish and their size distribution can, for most purposes, be considered as typical of the whole redfish area of the Gulf of St. Lawrence. It can be seen that these length-frequencies are characterised by a constant peak at about 35 cm for males and 38 cm for females. These peaks can be recognized in the length-frequencies from different areas in the Gulf and in different years. In the early years of the fishery these peaks, which represent the accumulated stocks of old fish, were made up of large numbers of fish, but more recently the numbers of these large fish caught per unit of effort has declined, so that in some areas the peaks are only just discernible. It should be noted that, although the numbers of fish in the length-frequencies are expressed relative to numbers caught per hour of fishing, the direct comparison of abundance between different years is only valid for the years 1959, 1960, 1961 and 1962.

In the years previous to 1959 not only was a smaller ship with its smaller associated net used, but the sets were not necessarily repeated at the same depth and position. In 1948 the ship was on most occasions likely using too little warp for the speed of tow, and most of the catches probably bear little resemblance to the true abundance of redfish. No fine-meshed liner was used at this time.

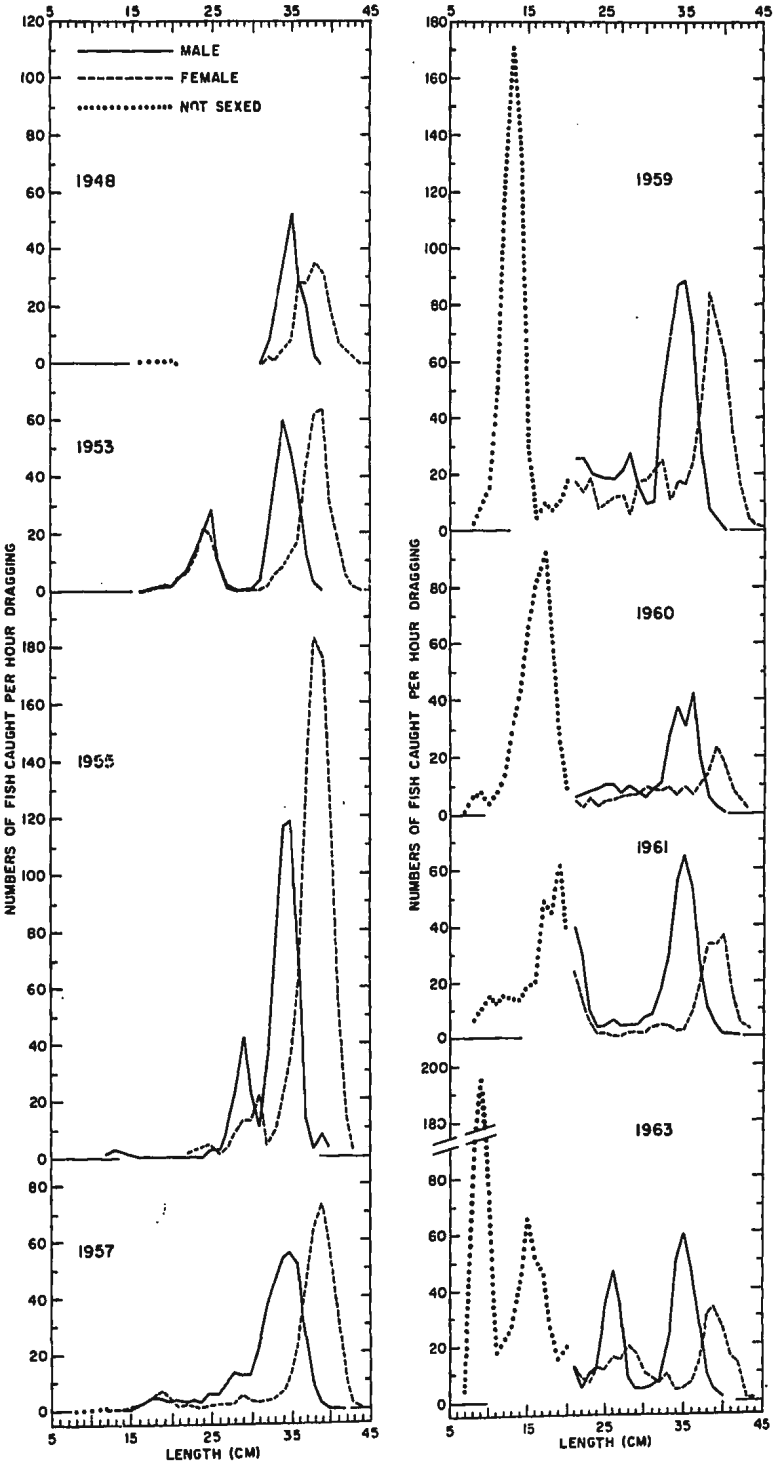

FIGURE 4.2 LENGTH-FREQUENCIES OF REDFISH FROM THE AREA OF LINE D GULF OF ST. LAWRENCE.

In addition to the stationary peaks of large fish, other peaks, which are made up of smaller, more rapidly growing fish, often occur. These latter peaks may, under suitable circumstances, be followed till they lose their identity when they merge with the peak of slower growing fish above them. In Fig. 4.2 the peak with males and females at about 24-25 cm in 1953 has progressed in 1955 to 28 cm for males and 31 cm for females, and in 1957 both the sexes have merged with the accumulated stock of old fish and are probably represented only by a bump on the ascending limb of this peak.

The fact that such peaks can be distinguished in a population of fish which has such a slow growth-rate is indicative of a rather tragic circumstance, namely that some or very few young fish have been recruited to the population for several years. This point is further emphasised in the length distribution of the fish caught in 1955 and 1957 which indicates, apart from the small and rather insignificant sign of one at 18-19 cm in 1957, a relative failure of year-classes for some 8 or more years after the success of the year-class which dominates the group of fish observed at about 25 cm in 1953.

Probably the most striking feature of Fig. 4.2 is the appearance of a new group of fish in 1959. The progression of this group with modal length of 13 cm in 1959 can be followed through the years 1959, 1960, 1961 and 1963. This group of fish, which consists mostly of a single year-class and which was observed in such numbers in the fall of 1959, was probably three years old at this time, and by 1963 when it was seven years old it showed a modal length of 26 cm for males and 28 cm for females. Although by far the majority of the fish making up the peak between 8 and

16 cm in 1959 were most probably three years old, there were nevertheless a few 2 and 4 year old fish included.

In 1959 only 4 of the major survey areas were examined, and it is interesting to note that in the areas where best catches of the larger redfish were obtained (Line E) so also were the best catches of this new group. Furthermore, the mode of this new group was at 15 cm, and thus 2 cm greater than that of the same group from line D in the Esquiman Channel.

It is unfortunate that there are some gaps in the data of these areas of greater redfish abundance, Lines E and F - east (Line E was not examined in 1963, Line F - west in 1961 and Line F - east in 1959 and 1961).

The length frequencies for these three lines are shown in Fig. 4.3. The dominance and abundance of the new, presumably 7-year-old group of fish and the relative insignificance of the large fish as shown in the graph for 1963 of Line F - east, and by inference presumably also Line E, is quite impressive. The abundance of this group is further emphasized by the catch obtained in one set at 155 fathoms on Line F - east in 1963, when in a 30-minute tow, 6560 pounds of redfish were obtained. This weight was made up by a total of over 15,000 fish.

Figs. 4.2 and 4.3 also show how in the four different areas from which these catches were obtained, although the basic pattern of year-class survival remains approximately the same, the actual survival as reflected by abundance does vary considerably from one locality to another.

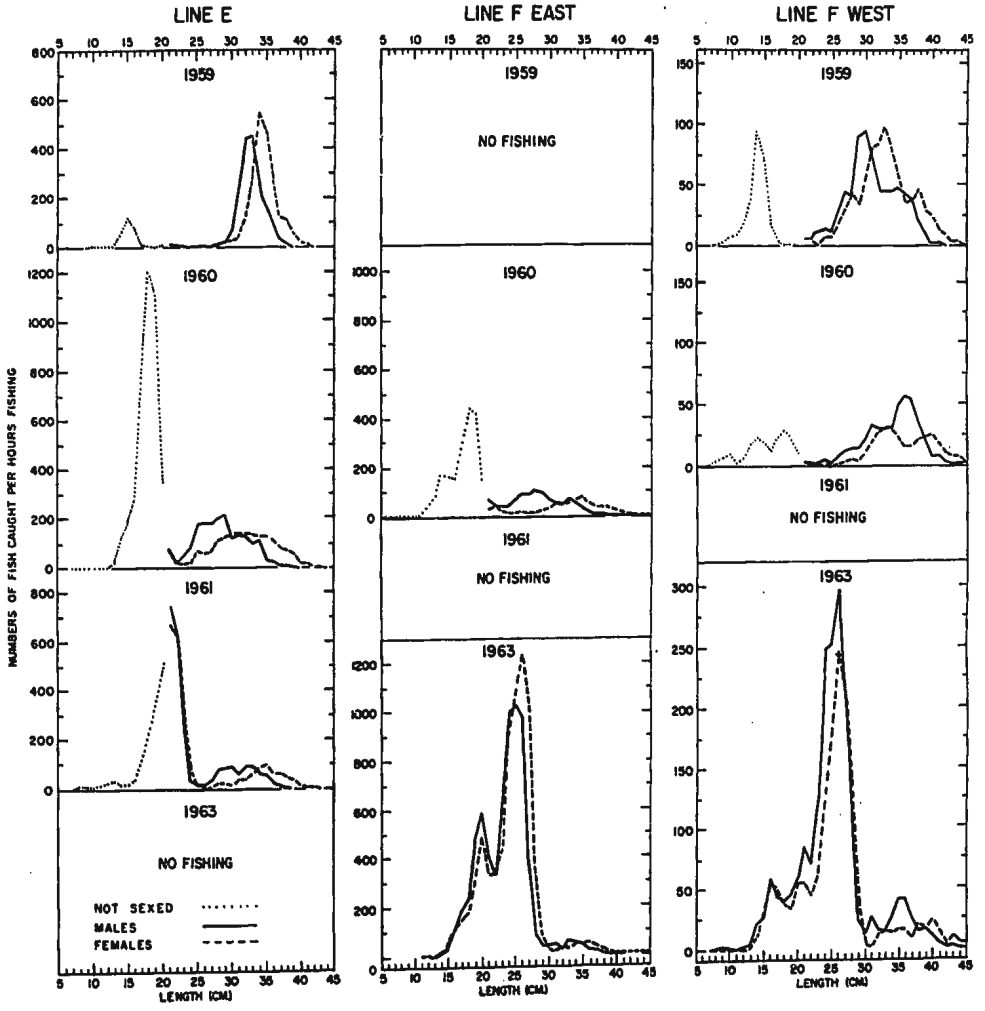

Figure 4.3 Redfish length-frequencies -- Gulf of St. Lawrence survey lines, E, F-east and F-west, 1959 to 1963. The numbers of unsexed fish have been halved to allow a direct comparison with the sexed fish.

This is illustrated by the comparison of the length-frequencies from Lines D, E and F-east. In Area D, and more so with Area E, the group first occurring in 1953 remains throughout the succeeding years dominated by a single year-class. Not so, however, in the case of Line F, where a more recent year-class, probably two years younger than the dominant one, has shown considerable strength; so much so in fact that the proximity of the two year-classes may affect the modes of the curves so that they may no longer represent the year-class modes. Thus polymodal curves must be examined with caution. Although it is still rather too early to say with any certainty, it would seem that the extremely abundant group at 9 cm from Line D in 1963 occurs in any quantity only in this area, and in other areas only indications of the group are to be seen.

A preliminary appraisal of the otoliths from samples obtained in 1959 from Line D indicates that the majority of fish of the dominant group at 13 cm were 3 years of age. If this is used as a base and the assumption made that the mode represents the mean of this dominant year-class, it is possible to obtain an approximate growth curve over the 5 years in question. This has been done for several areas in the Gulf of St. Lawrence in Fig. 4.4. Also shown in this figure is a composite plot for the Gulf area, where the modes for each year have been averaged. The curve drawn in the figure was obtained by fitting a curve to the average modal values of unsexed fish for 1959, 1960 and 1961, an interpolated point for 1962 and the mean modal length for males in 1963. The equation for this curve is given below

$$l_t = 58 \left\{1 - e^{-0.08\ (t + 0.7)}\right\}$$

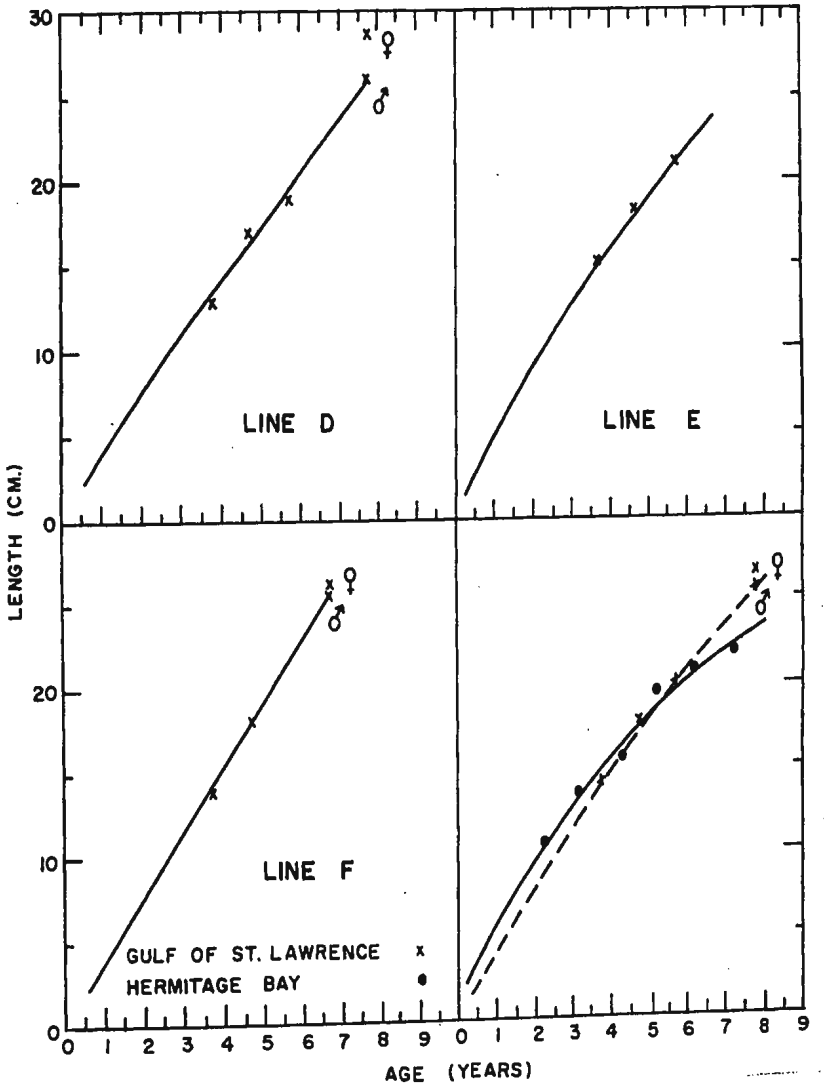

FIGURE 4.4 GROWTH CURVES FROM THE MODES OF THE DOMINANT GROUP IN THE GULF OF ST. LAWRENCE. IN THE LOWER RIGHT THE MODAL LENGTH VALUES FROM EACH LINE HAVE BEEN AVERAGED TO GIVE A COMPOSITE PLOT FOR THE AREA. THE FITTED BERTALANFFY CURVE IS SHOWN AS IS ALSO THE CURVE SHOWING THE GROWTH OF THE 1953 YEAR-CLASS IN HERMITAGE BAY

Also shown for comparison are the observed data points and fitted curve for the growth of the 1953 year-class in Hermitage Bay (Section 2).

The growth of the 2 year-classes in the Gulf of St. Lawrence and Hermitage Bay are rather similar, although the Gulf fish have continued to grow at their pre-maturity growth rate longer and have not shown any great tendency, as yet, for the curve to start flattening out as it starts to approach the asymptotic value. This is reflected in the very much higher L_{oo} which was obtained from the Gulf fit as compared to that of Hermitage Bay.

4.3 Growth from otoliths

4.31 Materials and methods

As has been already mentioned, the research ship Investigator II had visited the Gulf of St. Lawrence in 1947, 1948 and 1949, in fact, in the years before the start of any commercial fishery. Although the otolith collections from these early trips were not very extensive, they did provide a means of estimating the age distribution of the population at a time when mortality from causes other than natural was negligible. Thus it was hoped that, from the ages of these fish caught in pre-commercial days, we should be able to obtain an estimate of the natural mortality rate of the redfish population.

For the above reason the samples of otoliths examined were initially all taken from the earliest years of our collections. To obtain large enough samples to derive even an approximate age-length key, it was necessary to combine several samples of otoliths.

In doing this an attempt was made to obviate, as far as possible, any effects of different growth-rates in different areas of the Gulf by using only samples from the area of the Esquiman Channel (preferably Line D). As can be seen from Fig. 4.1 this was not always possible, and the occasional sample from other areas has also been included. Because of the complete dearth of small fish in the early years, it was decided that we should include a more recent sample containing some small fish. These would greatly improve the Bertalanffy fit for growth curve purposes, while for age frequency and mortality rate examinations they could be ommitted. The age estimations were all made by E. E. Squires.

4.32 Growth curves of the adult redfish

The mean lengths of male and female redfish have been plotted separately for each age group in Fig. 4.5. The curves represent the unweighted least squares fit to the smoothed data for even ages from 12 - 46.

The parameters of the curves shown in Fig. 4.5 together with their standard error are shown below:

Parameter	Males	Females
L_{oo}	36 ± 13	38.4 ± 1.2
K	0.06 ± 0.04	0.13 ± 0.04
t_o	- 5 ± 18	+ 4.4 ± 2.0

The rather wide confidence limits, particularly for the males, are largely due to the extreme paucity of data for the younger age-groups.

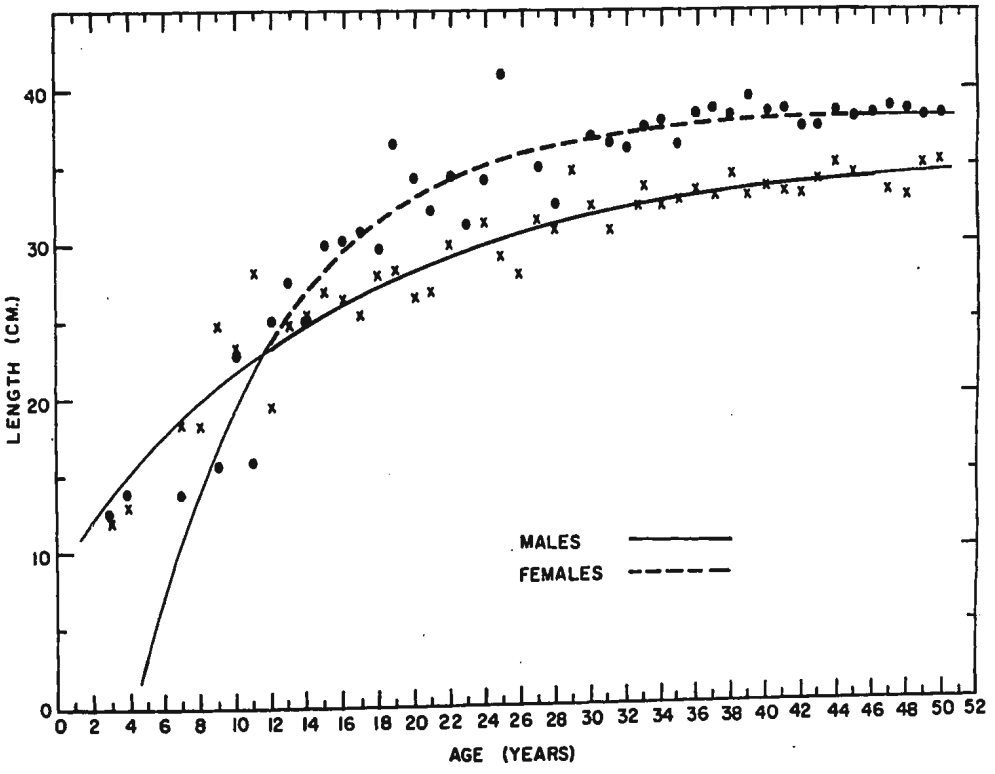

FIGURE 4.5 GROWTH CURVES OF REDFISH - GULF OF ST. LAWRENCE.

5 Flemish Cap

5.1 Introduction

The redfish fishery on Flemish Cap is of very recent origin. Redfish were shown to be present in the area in good commercial quantities by two cruises of the research vessel Investigator II in 1949 and 1950 when, during the latter cruise, two sets yielded catches of 10,200 and 7,400 pounds per hour. In spite of these large catches the area was considered to be too remote for exploitation by Canadian otter-trawlers which, during this the heyday of the virgin fishery, were able to fill up with fish in a very short time by fishing the nearer and more accessible areas. Thus the complete area of Flemish Cap remained unfished, except by the Investigator II, during the trips mentioned above and subsequent trips in 1953 and 1956, till the latter part of 1956 when the commercial fishery was started by the vanguard of the U.S.S.R. fleet.

The fishery rose rapidly from 54 metric tons in 1956 to a peak in 1958, when 54,532 metric tons was landed, almost entirely by vessels of the U.S.S.R. fleet. In 1959 the landings remained high at 52,208 but fell in the following year to only 8,419 metric tons. Since 1960 the landings have remained well below 20,000 metric tons.

It has been noted by Templeman and Sandeman (1957) that Flemish Cap is one of the localities in the Northwest Atlantic where catches can consist of both marinus and mentella redfish. As it was only during the trip to the area in 1956 and during subsequent trips that any separation of the types was made, we have not been

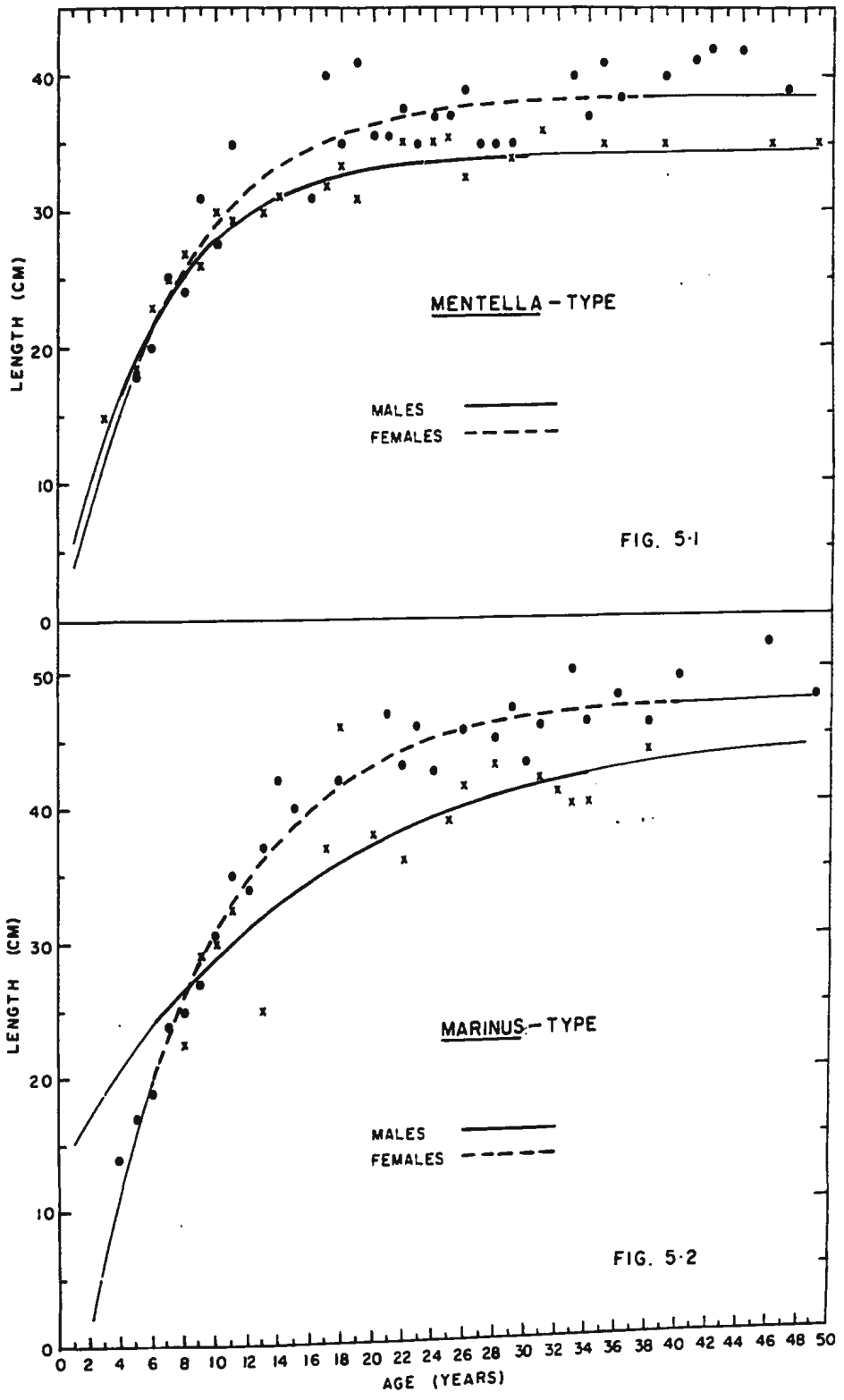

Figure 5.1 Growth curves of mentella redfish -- Flemish Cap.

Figure 5.2 Growth curves of marinus redfish -- Flemish Cap.

able to use otolith samples collected during the earlier trips to the area, and have had to be content with samples collected in 1956 or later.

Enough specimens of marinus redfish were obtained in the Flemish Cap area to allow a consideration of the growth-rate of these fish, as well as that of the more common and deeper living mentella.

5.2 Growth from otoliths

5.21 Material and methods

The fish, the otoliths of which were used in this study of age and growth-rate, were all caught on the northern slope of Flemish Cap. The fish caught in 1956 were taken by the research vessel Investigator II, while those obtained in November 1958 were caught by the A. T. Cameron. The otoliths obtained from these trips were from rather small samples of fish brought to the Biological Station for the purpose of making a detailed series of body proportion measurements and meristic counts. As can be seen in the table below, they were obtained from a variety of sets and depths, and because of the low number of otoliths obtained it has been necessary to combine the data from the different depths, and to include data obtained in a later trip to the area in 1958.

In addition to the samples being rather unsatisfactory numerically they are also somewhat unsatisfactory because they were selected to provide fish only at each length group of 5 cm or multiple thereof. Although this will, of course, affect the

Type	Date	Depth (fms)	Number of fish Males	Females
Mentella	July 1956	150	8	10
		200	8	5
		250	17	14
		300	8	15
	November 1958	250	12	18
			53	62
Marinus	July 1956	150	13	32
		200	2	2
	November 1958	150	14	22
		250	4	1
			33	57

Sources of data used in age determinations from Flemish Cap Area.

calculation of mean length at age, it is considered that the data are adequate for providing at least a preliminary examination of growth-rate.

The processing of the data from the fish and the otoliths remained as described in section 1.4.

5.22 Growth curves of adult redfish - mentella

The mean lengths at each age have been calculated and are displayed for males and females separately in Fig. 5.1. Also shown in this figure are the least squares Bertalanffy curves

fitted to the smoothed data for even ages from 4 to 30 for males and 6 to 40 for females. The parameters of the Bertalanffy curves, together with their 95% confidence limits, are tabulated below.

	Males	Females
L_{oo}	34.4 ± 1.2	38.5 ± 1.4
K	0.17 ± 0.05	0.15 ± 0.06
t_o	0.1 ± 1.2	0.6 ± 2.5

5.23 Growth curves of adult redfish - marinus-type.

The mean lengths at each age have been calculated and are displayed for males and females separately in Fig. 5.2. Also shown in this figure are the least squares Bertalanffy curves fitted to the smoothed data for even ages from 6 to 34 for males and 6 to 40 for females. The parameters of these fitted Bertalanffy curves, together with an indication of their 95% confidence limits, are tabulated below.

	Males	Females
L_{oo}	45 ± 14	47.8 ± 1.4
K	0.07 ± 0.10	0.13 ± 0.03
t_o	- 5 ± 8	1.9 ± 1.3

6. Hamilton Inlet Bank

6.1 Material and methods

The otoliths examined from the area of Hamilton Inlet Bank were all taken from fish caught by the research ship A. T. Cameron in August 1960. Fishing was carried out on a line across the slope at the northern part of Hamilton Inlet Bank (Fig. 1.1), where sets made at depths of 150, 175, 200, 250, 300 and 400 fathoms yielded catches of mentella redfish from which were obtained samples for otolith studies. In the set at 150 fathoms and in one at 140 fathoms, marinus were obtained. The numbers of fish of each type yielding otoliths and other data suitable for growth studies, and the depths from which these were obtained, are listed below.

Depth	mentella		marinus	
(fms)	males	females	males	females
140	-	-	47	19
150	7	9	34	48
175	61	47	-	-
200	76	37	-	-
250	54	54	-	-
300	61	41	-	-
400	4	11	-	-
Total	263	199	81	67

Age determinations were all by E. Squires.

6.2 Growth curves of mentella redfish

Growth curves for male and female redfish of this Hamilton Inlet Bank area (all depths combined) are shown in Fig. 6.1. The data points indicate the mean ages for each length group, and the curves shown are the least squares Bertalanffy curves fitted to the smoothed mean length data for even ages 6 to 38 for males, and 8 to 40 for females.

The parameters of the Bertalanffy equations and their standard errors are shown below.

Parameter	Males	Females
L_{oo}	38.5 ± 1.0	44.8 ± 2.1
K	0.16 ± 0.05	0.11 ± 0.04
t_o	- 0.1 ± 1.6	0.0 ± 3.1

When the curves are compared with the data points from which they are derived, it can be seen that they do not seem to fit the data very well. This is particularly so for the males, where ages 7, 8, 9 and 10 lie well below the fitted line and ages 16, 17, 18, 19, 20 and 21 lie above it, all of which would indicate a steeper slope at this section of the curve. As we have combined the data from such widely different depths, it is proper that any possible differences in growth with depth should be examined. Unfortunately, for each depth, the numbers of fish for which we have age data are rather small; however, provided we recognise this limitation, we can derive individual Bertalanffy curves for each depth.

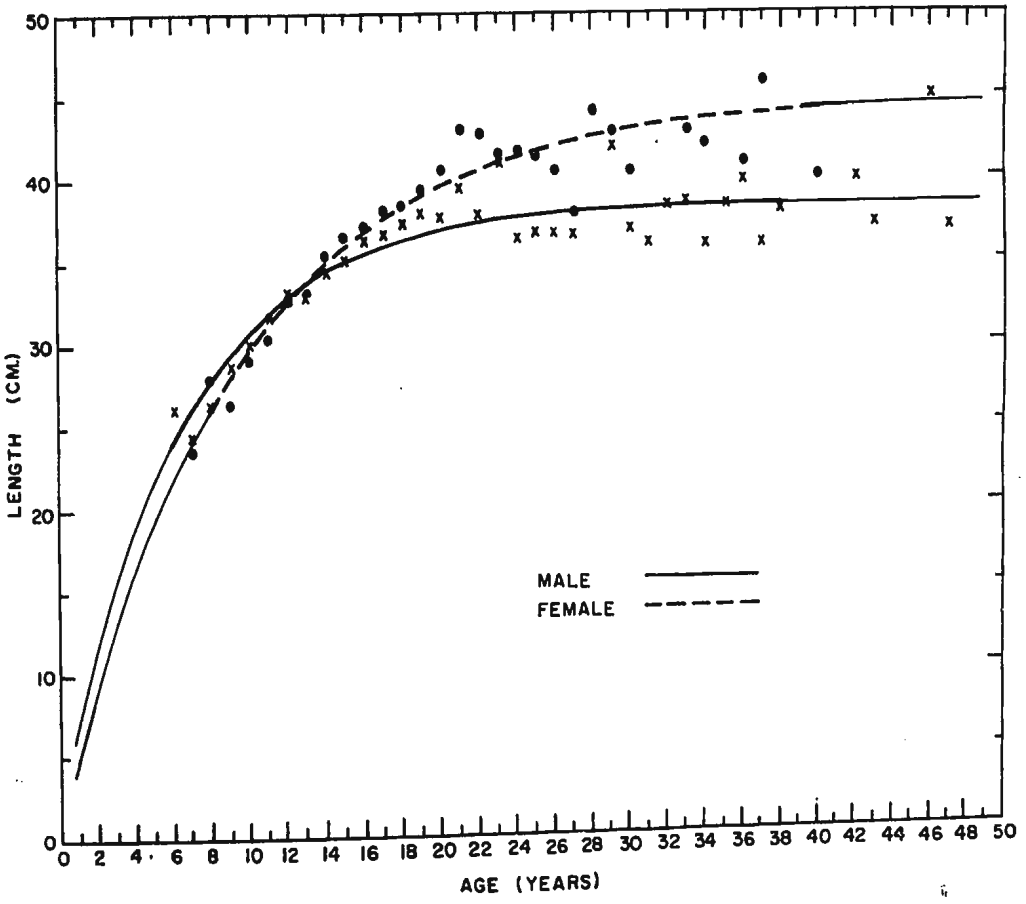

FIGURE 6.1 GROWTH CURVES OF SEBASTES REDFISH — HAMILTON INLET BANK. THE DATA FROM ALL DEPTHS HAS BEEN USED IN DERIVING THESE GROWTH CURVES.

6.21 Growth curves and depth - males

In examining the difference in growth from depth to depth, the few age data from 150 fathoms have been included with those for 175 fathoms and similarly the data for 400 fathoms with those for 300 fathoms. We now have the equivalent of four different depth levels, 175, 200, 250 and 300 fathoms. Bertalanffy curves have been fitted to the unsmoothed mean length at age data for each of these depths between the greatest range of ages for which we have mean lengths for consecutive ages. These were:

175 F	6	to	22 years
200 F	10	to	27 years
250 F	9	to	20 years
300 F	13	to	25 years

These curves are shown in Fig. 6.2. From this figure it would seem that the growth patterns of the fish from 175 and 200 fathoms are rather similar, and that these fish from the shallower depth ranges differ somewhat from those obtained from the deeper zones.

A perusal of the length-frequency distribution of the catches at the different depths shows a general trend of increase in size with increase in depth (Fig. 6.3). This trend, which may be seen in many localities in the Newfoundland area, together with the fact that the smaller fish are completely lacking from the greater depths, leads quite naturally to the hypothesis that the fish gradually move deeper as they grow larger and presumably older.

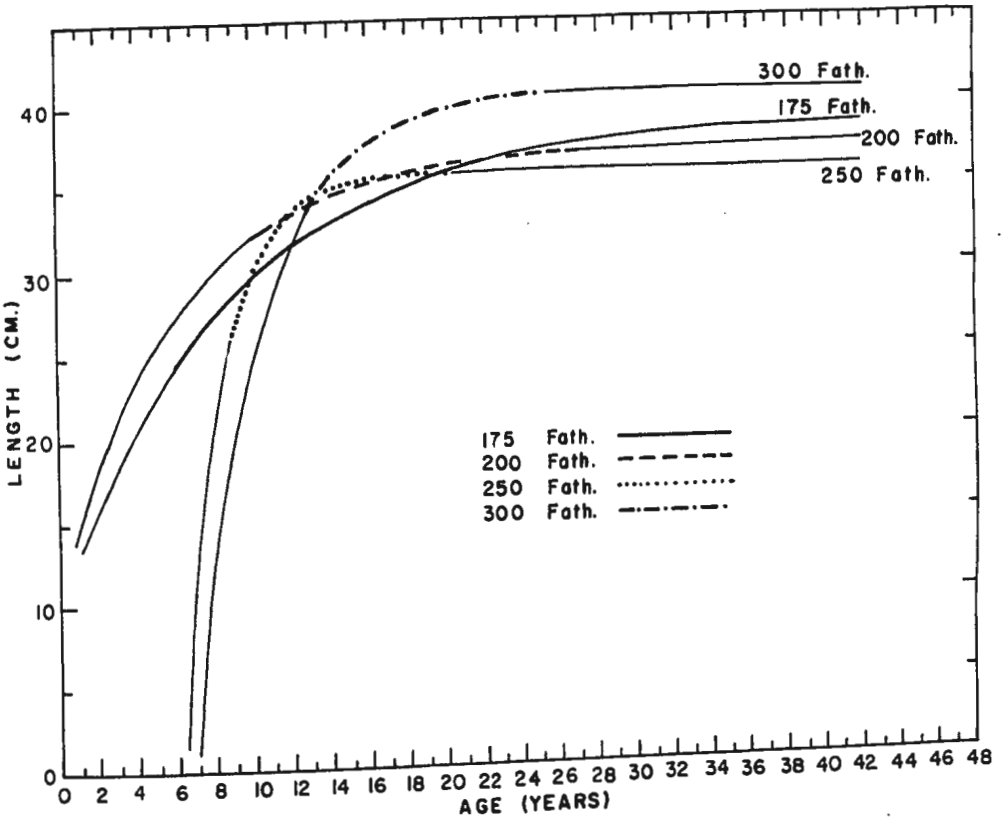

FIGURE 6.2 GROWTH CURVES OF MENTELLA REDFISH FROM DIFFERENT DEPTHS OF HAMILTON INLET BANK -- MALES.

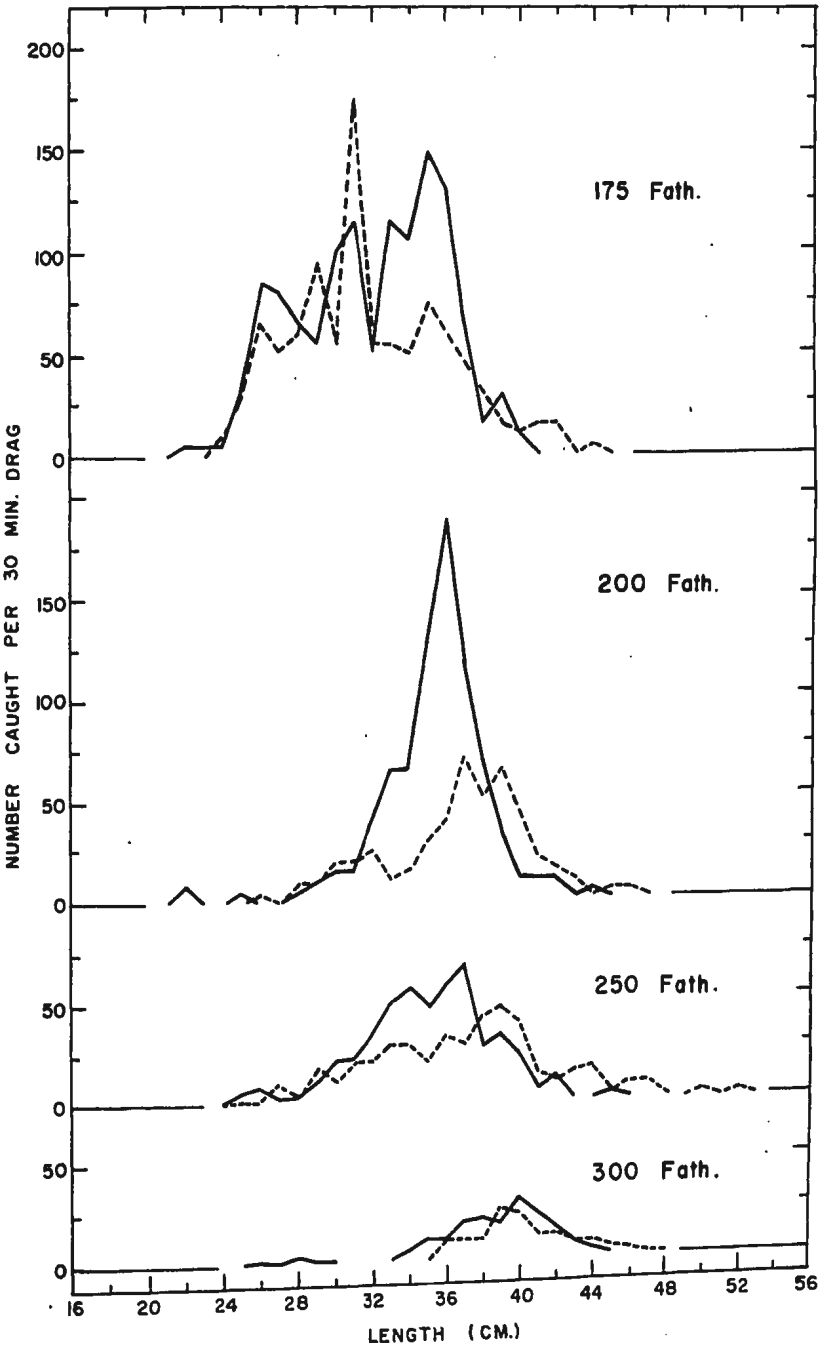

FIGURE 6.3 LENGTH-FREQUENCIES OF CATCHES FROM DIFFERENT DEPTHS OF HAMILTON INLET BANK -- MENTELLA REDFISH ONLY.

However, when the age frequency distribution (Fig. 6.4) of the catches at the different depths is examined, we can see that this is not the whole story. It is clear that most of the oldest fish in the catches occured in depths of 175 and 200 fathoms, whereas the largest fish occurred in greatest numbers in the deepest set, at 300 fathoms.

Fig. 6.5 presents the same age frequency data in a different way, and suggests that although the hypothesis above might well be correct between the depths of 175 and 200 fathoms, and also between 250 fathoms and 300 fathoms, there appears to be a basic difference between the deeper and shallower depths with a dividing line between 200 and 250 fathoms.

Thus it seems correct to combine the data from the depths of 175 and 200 fathoms for comparison against the combined data from 250 and 300 fathoms. This has been done, and the growth curves for the combined data are shown in Fig. 6.6. These Bertalanffy curves were fitted to the unsmoothed data from ages 10 to 22 in each case.

The results shown in Fig. 6.4, 6.5 and 6.6 suggest that we have here two separate populations of redfish which, although they originate from the same shallow water population of young fish, have become separated from each other at an age of about 10 - 12 years to form a shallow water stock of slow-growing fish and a deep-water stock of fast-growing fish. Further evidence of the separate identity of the stocks at these two depth levels is provided by the sizes and ages of first maturity. Although the numbers of immature fish are rather small relative to the numbers of mature fish, there are sufficient immature fish to demonstrate this point.

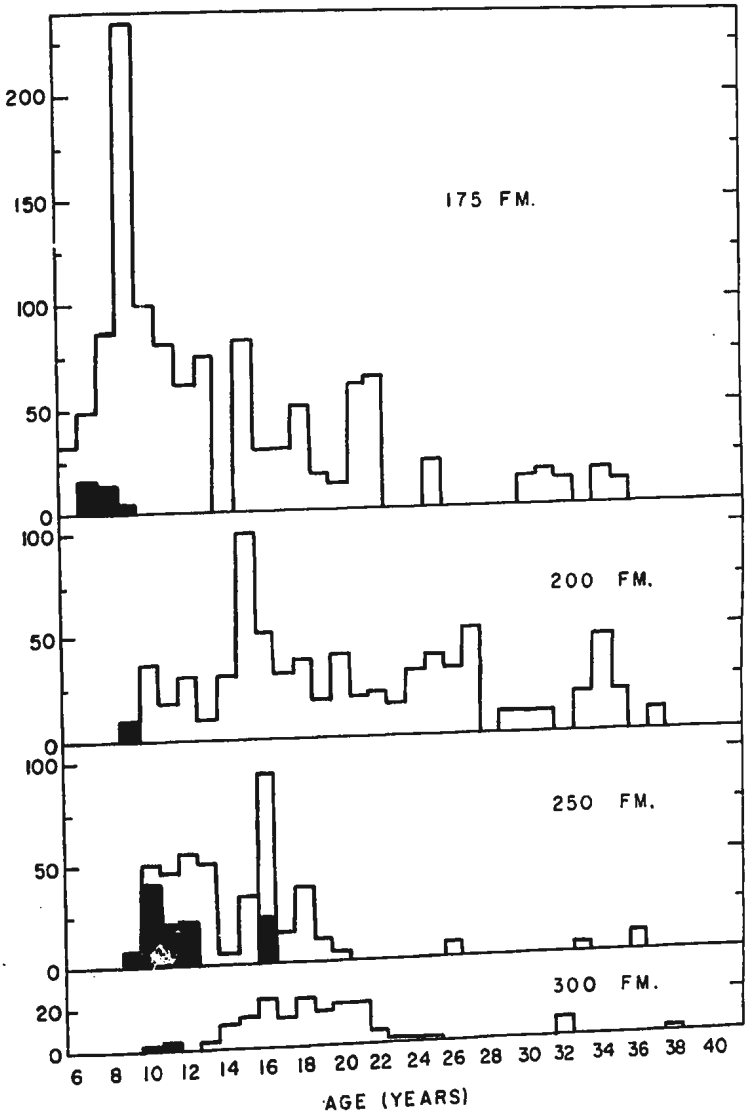

FIGURE 6.4 AGE-FREQUENCIES OF MENTELLA FROM DIFFERENT DEPTHS OF HAMILTON INLET BANK -- MALES. (SHADED PORTION SHOWS IMMATURE FISH).

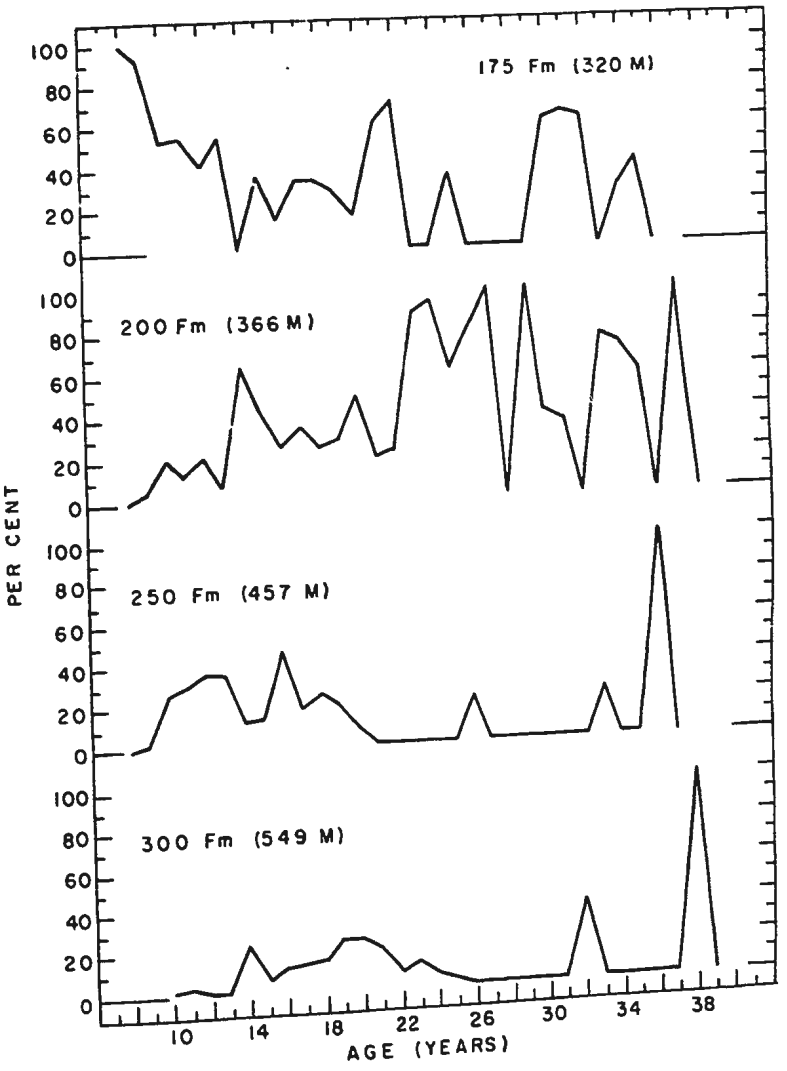

FIGURE 6.5 PERCENTAGE OF TOTAL NUMBER HENTELLA (ALL DEPTHS) AT EACH AGE, WHICH OCCUR AT EACH DEPTH ON HAMILTON INLET BANK -- MALES.

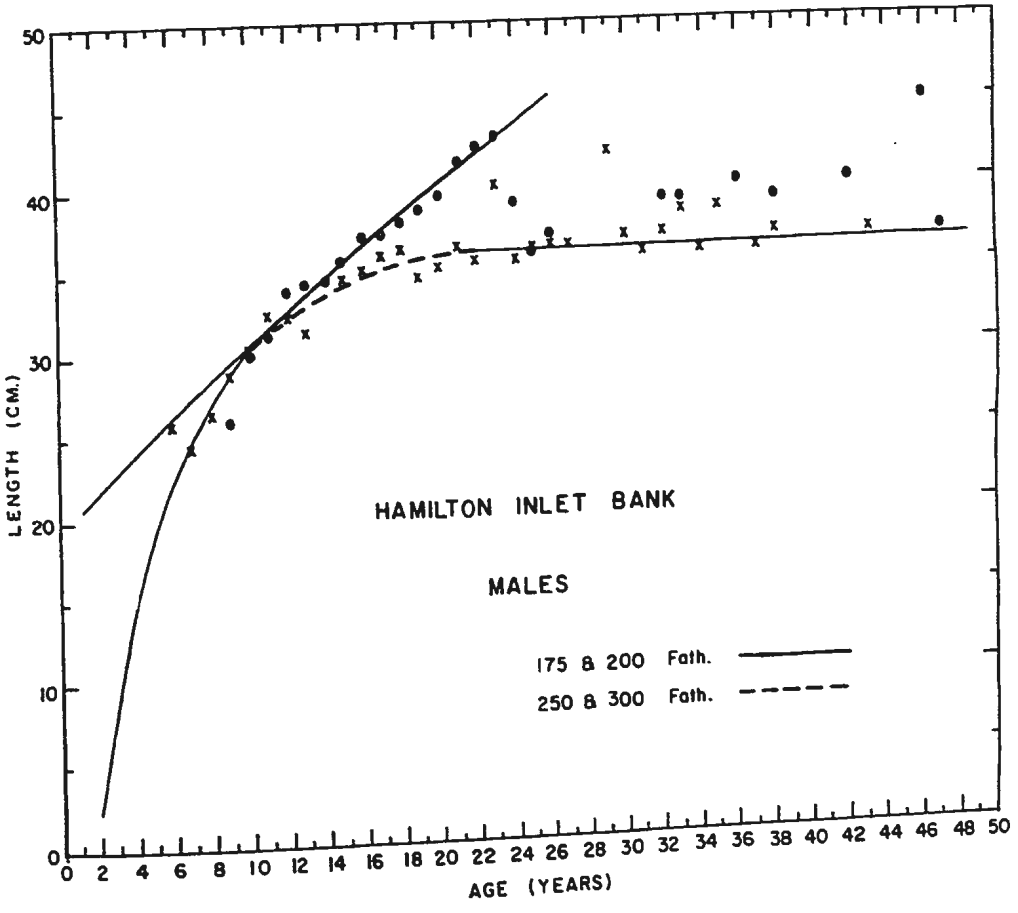

FIGURE 6.6 GROWTH CURVES OF MENTELLA REDFISH FROM THE SHALLOWER (175-200 Fm.) AND DEEPER (250-300 Fm.) DEPTH ZONES OF HAMILTON INLET BANK -- MALES.

Whereas in the 175 and 200 fathom levels mature fish were more abundant than immature fish at lengths of 25 cm and greater, in the 250 - 350 fathom levels mature fish only outnumbered immature fish at lengths of 33 cm and greater. With regard to age, at the shallower depths mature fish outnumbered the immature fish at all ages encountered in the catch, (age 6 onwards) whereas in the deeper sets the mature fish did not outnumber the immature fish till about age 12.

It might be noted that although the hypothesis above suggests the existence of two stocks of redfish having different growth and maturity characteristics, these stocks need not remain separate at all stages of their annual cycle. The hypothesis, based as it is on growth and differences in growth-rate, requires a separate identity to the stocks only during the period of active growth, and does not preclude a mixing of stocks or change in depth level of either stock at any time of the year when growth, and presumably also active feeding, are not taking place.

6.22 Growth curves and depth - females

When the data for the female redfish are treated in the same way as for the males above, and Bertalanffy curves fitted between the following ages:

175 F	7 - 20
200 F	10 - 20
250 F	11 - 21
300 F	14 - 26

the curves shown in Fig. 6.7 are obtained.

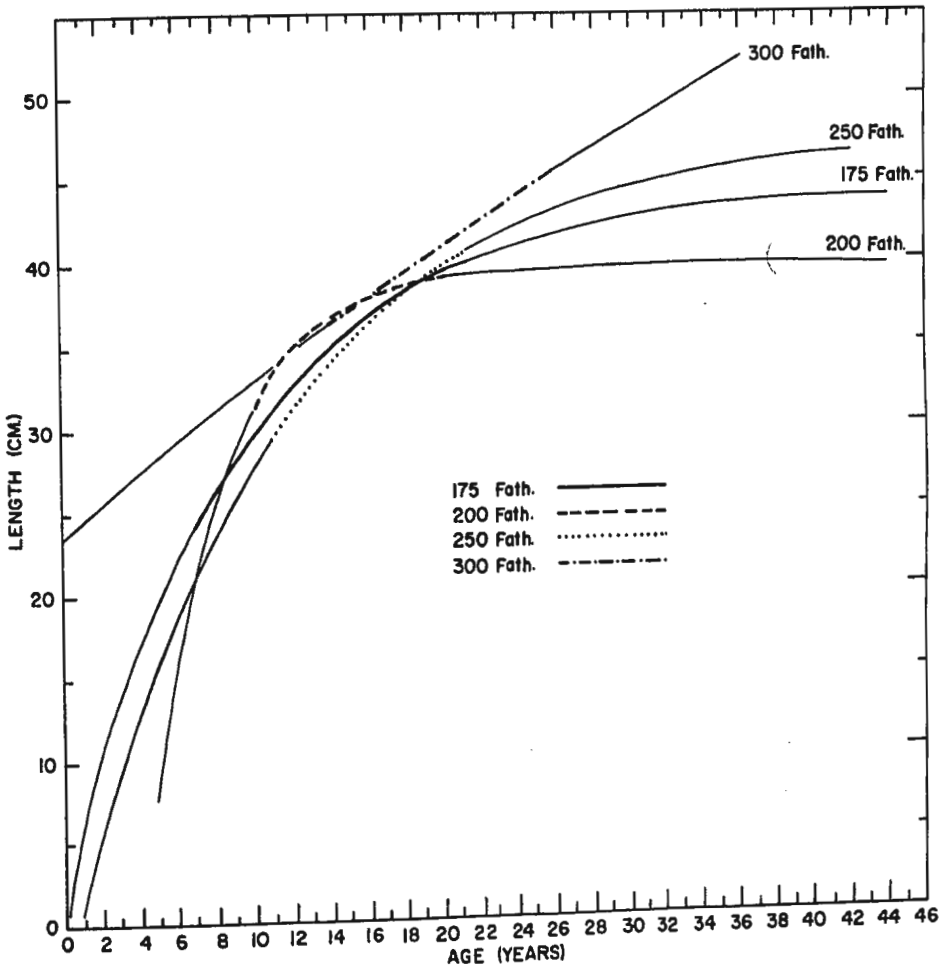

FIGURE 6.7 GROWTH CURVES OF MENTELLA REDFISH FROM DIFFERENT DEPTHS OF HAMILTON INLET BANK -- FEMALES.

Although a difference in growth between the deeper and shallower caught fish can be seen in this figure, the hints of a clear-cut separation between fish of the two depth zones that were apparent when the growth patterns of the males were being considered, cannot be as clearly recognised. However, examination of the length-frequencies (Fig 6.3) together with the age-frequencies (Fig 6.8), and particularly the maturity structure of the fish caught at the different depths, indicates that a similar separation of the females into two populations having differing growth characteristics exists, as it did for the males.

Consequently the data from 175 and 200 fathoms have been combined as have also those for 250 and 300 fathoms. The Bertalanffy curves for these two depth zones are shown in Fig 6.9. The Bertalanffy curves were fitted to the unsmoothed data for all available consecutive ages at each depth zone; these were 7 to 20 years for the shallower depth zone and 11 to 22 years for the deeper. Figure 6.9 indicates that, although they may grow to greater sizes during the earlier years of life in the shallower depths, if the fish remain in these depths they will not be as likely to grow as fast or attain such sizes as they would if they moved to the zone of greater depth.

6.23 Differences in growth-rate with depth.

From the growth curves shown in Fig. 6.6 and 6.9, some idea can be obtained of the growth-rates prevailing in the catches at the two depth zones and their respective rates of decrease.

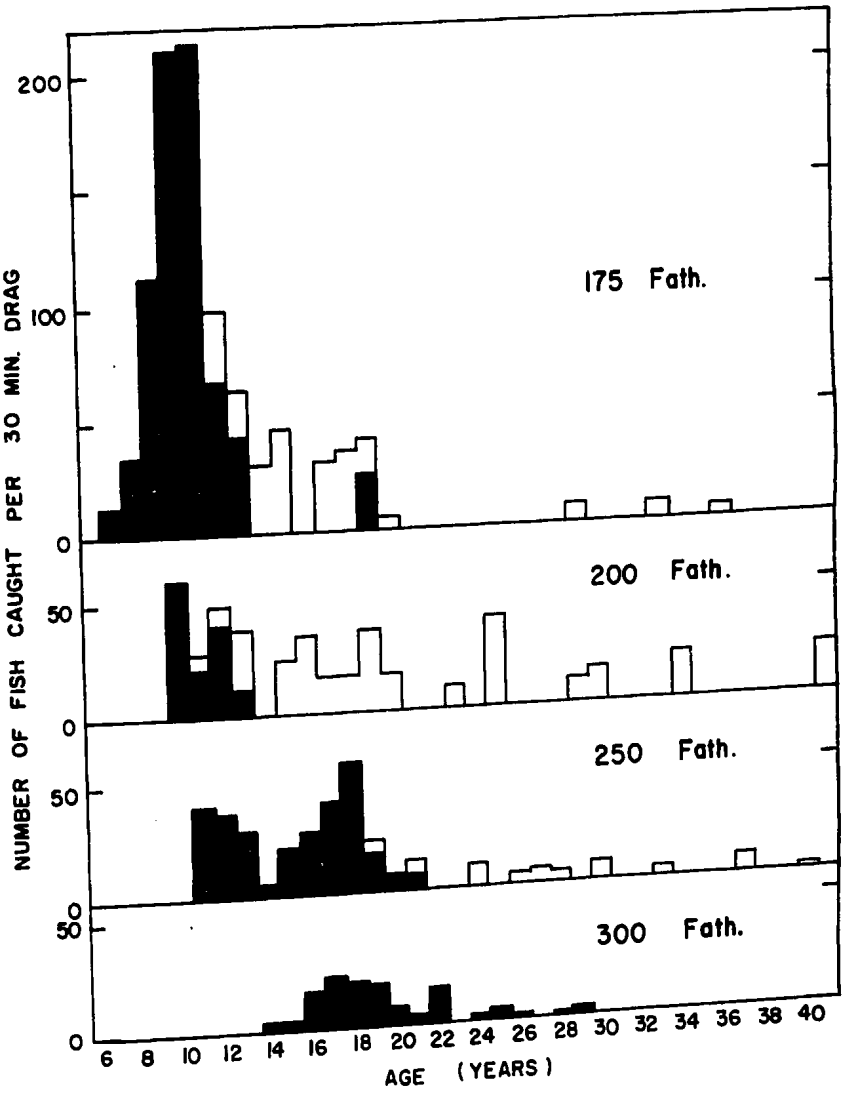

FIGURE 6.8 AGE-FREQUENCIES OF MENTELLA FROM DIFFERENT DEPTHS OF HAMILTON INLET BANK -- FEMALES. (SHADED PORTION SHOWS IMMATURE FISH).

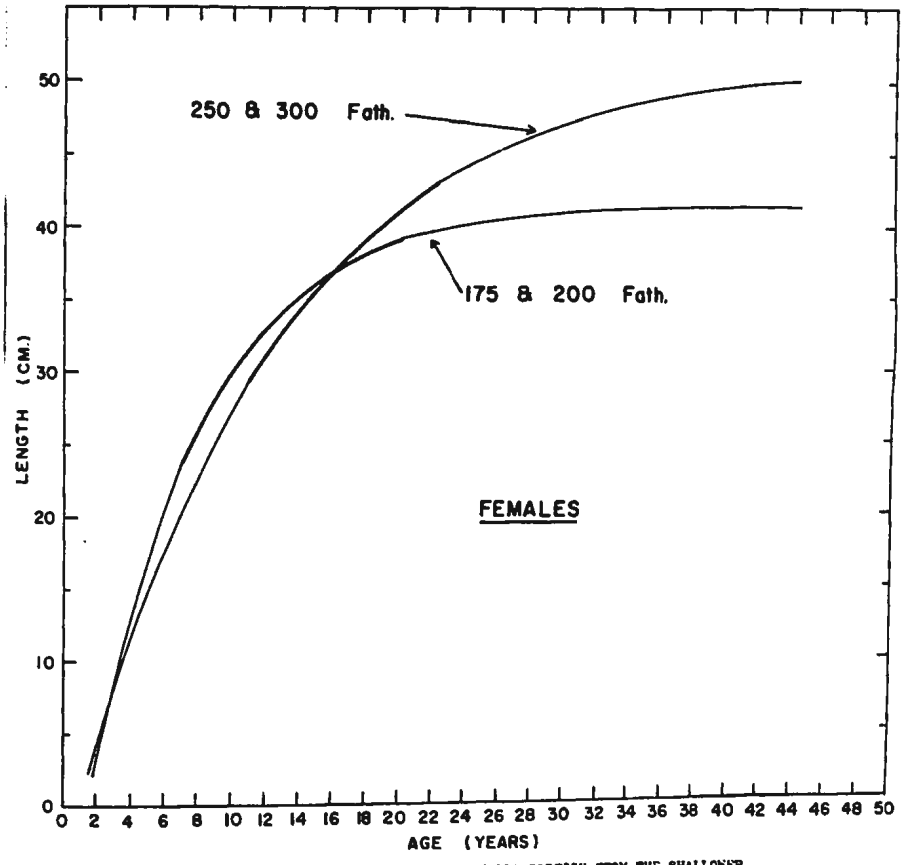

FIGURE 6.9 GROWTH CURVES OF *SEBASTES* REDFISH FROM THE SHALLOWER (175-200 Fm.) AND DEEPER (250-300 Fm.) DEPTH ZONES OF HAMILTON INLET BANK — FEMALES.

(The latter is represented by the parameter of the Bertalanffy equation K, and the former by the slope of the growth curve at each point along it). However, if it is only growth-rate that is being considered, the direct comparison of the different growth-rates can most easily be accomplished graphically by the plot of instantaneous growth-rate against either fish length or time (age). This has been done to compare the growth-rates at the two depth zones for males and females separately in Fig. 6.10. It is clear from these plots that, both for males and females, the growth-rate is higher for the younger ages at the shallower depths, whereas the older fish show faster growth in the greater depths. It is also evident that, if the theoretical curves provide reasonable expectations of growth, and provided other things remain equal, maximum growth-rates will be obtained if the males migrate from shallow to deep water at about their 11th year and females at about their 9th.

If we accept a difference in growth-rate between the deep and shallow depth zones it is of interest to examine briefly what might cause such a difference. In general this difference might be due to either or both of two basic types of causes. The one consisting of factors of the fish themselves, and the other of factors stemming from the environment.

Concerning the physiology of the fishes, we have already noted that one of the main features indicating the differences in growth pattern between the depth zones was that of maturity. In particular it was noted that the age of first maturity was considerably delayed in the deeper zone, so much so in the females in fact that no mature fish were found in depths of 300 fathoms or deeper.

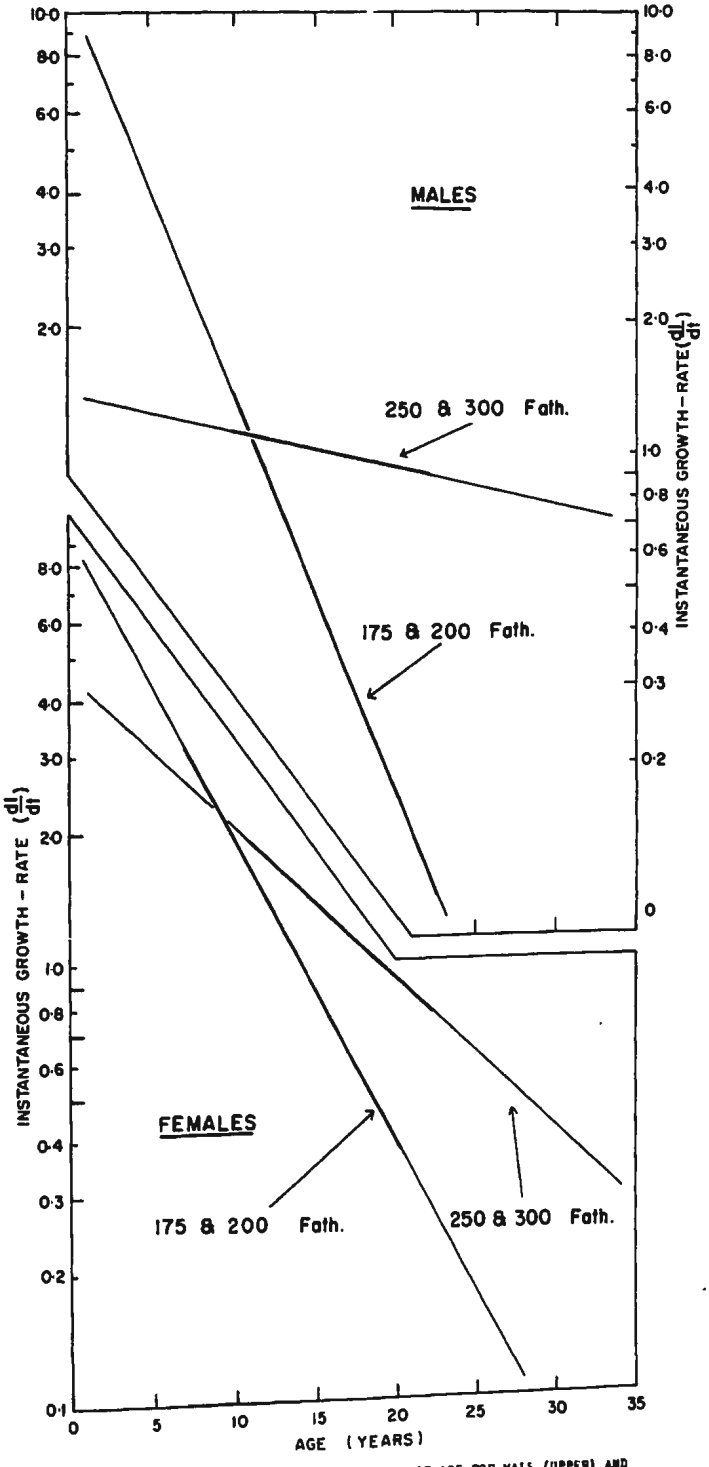

FIGURE 6.10 PLOTS OF GROWTH-RATE AGAINST AGE FOR MALE (UPPER) AND FEMALE (LOWER) MANTELLA FROM THE SHALLOWER (175-200 Fm.) AND DEEPER (250-300 Fm.) DEPTH ZONES OF HAMILTON INLET BANK. THE ORDINATE SCALE IS LOGARITHMIC.

It would thus seem possible that the change in growth-rate apparent between the two zones is not so much an increase in growth-rate as the fish change from one form of Bertalanffy growth to another, but rather a decrease in growth-rate in the shallow zone caused by the larger and older fish attaining maturity, and devoting much of their growth energy to the exigencies of reproduction, while their relations, who emigrated to the deeper zone, continue to live and grow as adolescents. However, much as this is an attractive hypothesis, it is evident from the maturity pattern of the males that, in spite of maturity being attained in the deeper water, growth continued at the fast rate that prevailed before maturity.

An environmental factor which has a very close relationship with metabolism and growth is that of temperature. The prevailing temperatures however, in these waters of 175 fathoms or deeper, remain very stable from depth to depth, and indeed also from year to year, and thus could not really be expected to affect the growth-rate. It is possible however that the closer proximity of the cold water layers to the shallower depth zone could limit the foraging area, and that the pelagic feeding habits of these fish have not the scope and range that is available to the fish from the deeper zone.

The most likely cause of the faster growth-rate in deep-water is probably to be found in the interplay of environment and fish physiology that occurs in the process of feeding. Here, unfortunately, we have but very little data, and until Mr Rees has finalised his studies on the food and feeding of redfish we can add nothing constructive to the problem, apart from quoting

the generalisation that with increase in depth redfish tend to eat more and more fish as opposed to the smaller invertebrates which make up their diet in shallow water. (Rees, MS. 1962.)

6.3 Growth-curves of marinus redfish

Although the numbers of specimens of fish yielding otoliths for age and growth studies were rather small, growth curves have been fitted to the age estimates of the 81 male and 67 female marinus redfish. The mean ages at each length and the fitted Bertalanffy curves are shown in Figure 6.11. The curves were fitted to the smoothed means of even ages from 18 to 42 for both males and females.

The parameters and their standard errors are shown below.

	Males	Females
L_{oo}	55 ± 9	60 ± 6
K	0.05 ± 0.06	0.10 ± 0.12
t_o	-9 ± 14	4 ± 18

It is to be noted that only three fish with ages less than 18 years occurred in our random sample.

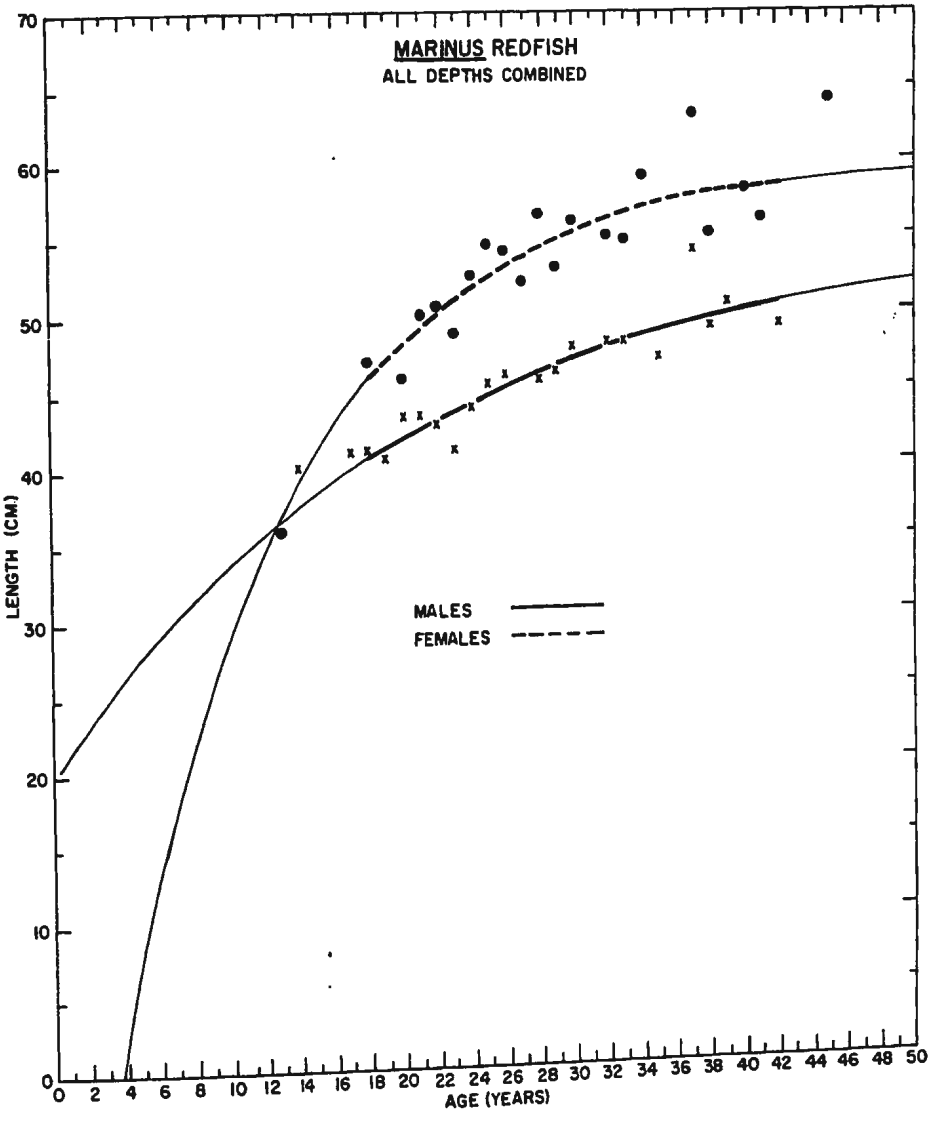

FIGURE 6.11 GROWTH CURVES OF MARINUS REDFISH -- HAMILTON INLET BANK.

7. Comparison of growth-rates of redfish in the Newfoundland area - St John's data

In the previous Sections 2 to 6, growth curves have been presented showing the growth patterns of redfish in 5 different areas around Newfoundland. It is now necessary to compare these growth curves and to examine how and, if possible, why the growth-rates vary from locality to locality. Before doing this, some attention should be devoted to differences in growth that are apparent between the sexes.

7.1 Differences in growth-rate between males and females

7.11 Mentella redfish

In all the growth curves presented in Sections 2 to 6 of this paper, it is apparent that a striking difference in growth pattern exists between the sexes. The growth of the females is nearly always greater than that of the males, and at any of the later ages the females are on the average very much larger than the males. A perusal of the parameters of the fitted Bertalanffy curves (Table I) in conjunction with the 95% confidence limits indicates that the main difference between the growth of the sexes lies not so much with the parameter K, but with L_{oo}. Here, it may be observed that in the areas of Hermitage Bay, Flemish Cap and Hamilton Inlet Bank the confidence limits of L_{oo} for the males and females do not overlap, and this indicates that the differences are likely to be real. In the areas of the Gulf of St. Lawrence and Southwest Grand Bank, the difference between the L_{oo} values for the males and females is less than 3 cm, and we cannot

Table I

Mentella redfish

		K		L_{oo}		t_o		Fitted years	
Hermitage Bay									
Males	*	0.119	0.028	35.2	1.0	-0.3	1.6	6	40
Females	*	0.113	0.019	39.7	0.9	0.2	1.0	6	40
Southwest Grand Bank									
Sandeman									
Males	*	0.05	0.05	33	6	-20	6	8	34
Females	*	0.13	0.05	34.2	1.4	-0.7	3.0	8	32
Squires									
Males	*	0.06	0.04	30.6	2.3	-17	5	8	34
Females	*	0.13	0.07	33.3	2.0	-1	5	8	34
Gulf of St. Lawrence									
Males	*	0.06	0.04	36	13	-5	18	12	46
Females	*	0.13	0.04	38.4	1.2	4.4	2.0	12	46
Flemish Cap									
Males	*	0.17	0.05	34.4	1.2	0.1	1.2	4	30
Females	*	0.15	0.06	38.5	1.4	0.6	2.5	6	40
Hamilton Inlet Bank									
All depths									
Males	*	0.16	0.05	38.5	1.0	-0.1	1.6	6	38
Females	*	0.11	0.04	44.8	2.1	0.0	3.1	8	40
175+200 F.									
Males		0.21		36.5		2		10	22
Females		0.16		41.5		2		7	20
250+300 F.									
Males		0.02		93		-14		10	22
Females		0.08		52		1		11	22

Marinus redfish

Flemish Cap									
Males	*	0.07	0.10	45	14	-5	8	6	34
Females	*	0.13	0.03	47.8	1.4	1.9	1.3	6	40
Hamilton Inlet Bank									
Males	*	0.05	0.06	55	9	-9	14	18	42
Females	*	0.10	0.12	60	6	4	18	18	42

* denotes when fit was made to smoothed data for even years.

Table I. Summary table showing the Bertalanffy parameters and their standard errors.

consider purely on the basis of the parameters and their confidence limits that the parameters are different. However, it is to be noted that in both these areas the growth curves of the males are rather aberrant, and in each we have a rather large negative t_0 value. This results in a very much lower than usual K value and a slightly higher value for L_{oo}.

The difference between the actual growth-rates of the males and females can be better seen in Fig. 7.1. In this figure the plot of growth-rate against age is shown for males and females in each of the 5 areas examined. It is quite clear that in Hermitage Bay, Hamilton Inlet Bank and Flemish Cap the growth-rate of the females at all ages, is greater than that of the males. In the Gulf of St. Lawrence and on the southwest slope of the Grand Bank the females are faster growing than the males to an age of about 24-25 years, and after this the males grow faster than the females.

It seems likely that the difference in growth-rate between males and females is due not so much to the environment, but to the behaviour and physiology of the fish. The fact that the males mature at considerably smaller sizes and ages than do the females (in Hermitage Bay on the average, males mature at about 20 cm at which time they are about 6 years old, whereas females mature at about 30 cm or 10 to 12 years of age), suggests that the males will start earlier to divert energy to reproduction, with the probable result that less energy is available for growth. The fact also that the reproductive season for the males coincides with the latter part of the season of greatest growth (as shown in the curve of seasonal growth - Fig. 2.6), probably means that the growth season is shortened in effect for the mature males.

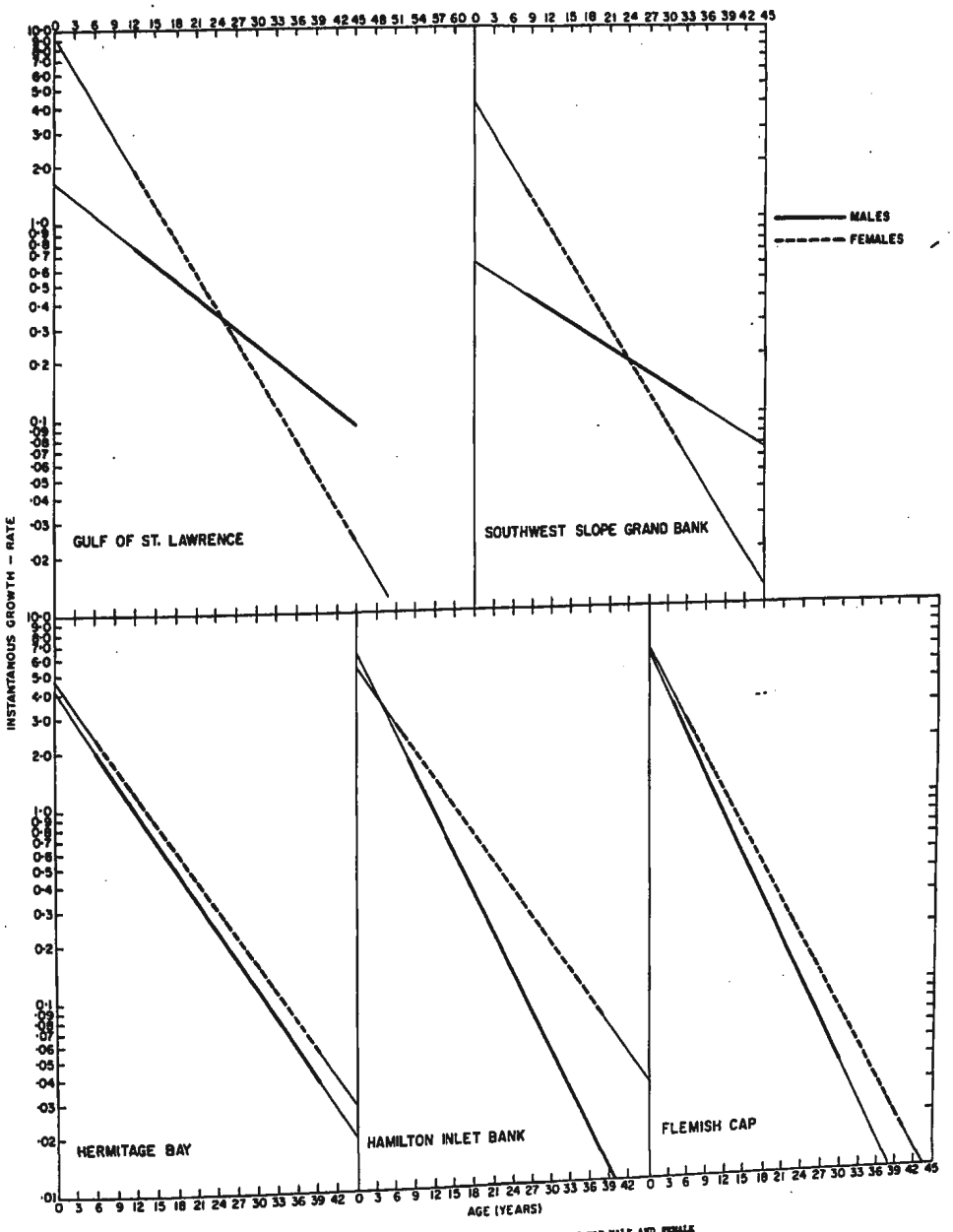

FIGURE 7.1 INSTANTANEOUS GROWTH-RATE AT EACH AGE FOR MALE AND FEMALE HADDOCK FROM EACH OF THE 5 AREAS EXAMINED.

Rees (MS, 1962) presents some evidence to show that in the Hermitage Bay area, the redfish feed most heavily in May and June, and then gradually reduce their feeding till November when their migration out of the area is usually well underway. The larger males show a rather dramatic drop in feeding during July - August, and after this in September their feeding once again becomes heavier. The reduction in feeding during July - August coincides with the pre-copulatory maturation phase of the males.

7.12 Marinus redfish

The difference in growth pattern between the sexes of marinus redfish resembles that observed for the mentella of the Southwest Grand Bank and the Gulf of St. Lawrence. The males in these two areas and the marinus males from both Flemish Cap and Hamilton Inlet Bank show Bertalanffy growth patterns involving fairly high t_o values and low values for K. The differences in growth-rates between the males and females, as well as between the two areas, can be seen in Fig. 7.2. It is apparent that in both these areas the females show higher growth-rates than the males during the younger years but, after about age 21 at Flemish Cap and age 33 at Hamilton Inlet Bank, the males exhibit faster growth. (It should be noted that in these plots of $\frac{dl}{dt}$ against t, the logarithmic scale of the ordinate distorts the appearance of the growth-rate, and that the higher growth-rates are compressed whereas the lower growth-rate values are expanded.)

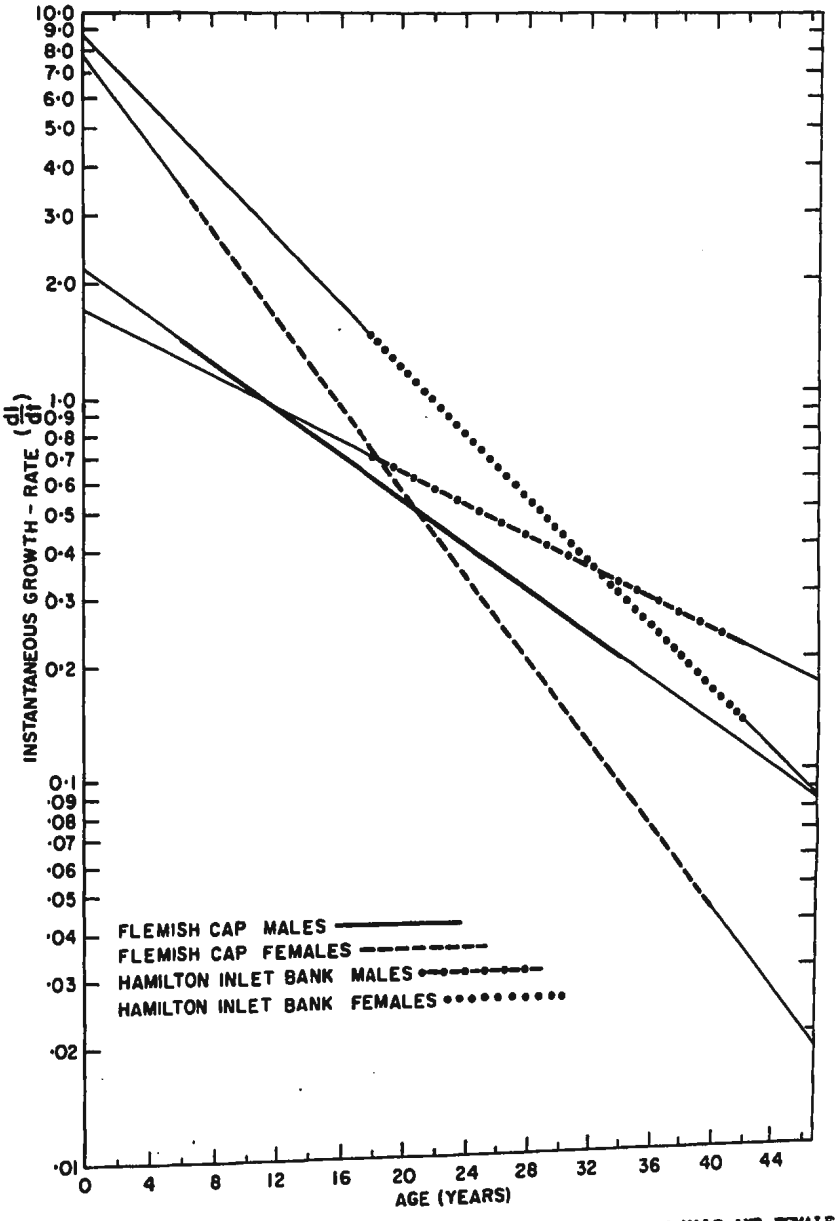

FIGURE 7.2 INSTANTANEOUS GROWTH-RATE AT EACH AGE FOR MALE AND FEMALE HARINUS AT FLEMISH CAP AND HAMILTON INLET BANK.

7.2 Comparison of the growth-rates

7.21 General considerations

Several different methods exist by which we might compare the growth of fish from a variety of areas. To show the different growth patterns by means of growth curves is useful, and from these curves the average lengths, at any age for any of the fish stocks being examined, can easily be seen and compared with those from other areas.

If the growth curves can be adequately described by the substitution of different parameters in a growth equation, then a comparison of these parameters might provide a satisfactory means of comparing growth. A very simple example can be seen in the case of linear growth when length (l_t) is related to age (t) by a simple straight line relationship

$$l_t = mt + c$$

where "m" is the rate of growth and "c" the length at zero age. The comparison of values of "m" and "c" from different areas would, with this type of growth, provide a very convenient means, not only of comparing the growth between different areas, but also of providing possible clues as to why these different growth patterns exist.

The Bertalanffy equation has been found to describe adequately the growth pattern of many species of fish, and several authors have examined the relations of the parameters of this equation to each other and to various environmental factors (in particular Beverton and Holt, 1959; Taylor, 1958, 1959 and 1960).

Of the relations between the parameters themselves, K and L_{oo} have been found and, indeed, according to Knight (M.S. 1962), may a priori be expected to show an inverse correlation with each other. When t_o has values which depart from zero, it will likely also be inversely correlated with K.

Concerning the possible relation between the Bertalanffy parameters and factors of the environment, and the possibility of using these parameters for comparing the growth patterns of fish from different areas, the whole matter is rather confused. Much of the confusion arises because the simple relationships between the parameters of the Bertalanffy growth equation and metabolism do not appear to be as simple as they first seemed.

Beverton and Holt (1957) reason that growth depends primarily on the food supply, which in turn is closely dependent on the population density. Because they are considering the subject from the point of view of population dynamics and the influence change in population density might have on growth, they consider that changes in population density will be large and, with a limited food supply, it is likely that the affect of population density on growth will outweigh that of all other factors. Thus they argue that K, which on theoretical grounds is independent of food consumption, will remain constant, and that changes in growth-rate may be represented by variations in W_{oo} or L_{oo}.

Taylor (1958, 1959 and 1960) examined the growth of cod, the Pacific cockle and the Pacific razor clam and found that K was positively correlated with temperature in each of these species. Holt (1959) discussed this relationship between K and temperature, and from a theoretical standpoint showed that while K would be expected to increase logarithmically with temperature, L_{oo} would

be expected to decrease rather slowly over the same range of increase in temperature.

Beverton and Holt (1959) state that the asymptotic size (L_{oo}) can be greatly modified by the supply of food available, but that this does not affect the parameter K.

Kinne (1960) examined the growth of Cyprinodon macularius at five levels of constant temperature, and it would appear from these data that not only does K increase with increasing temperature (Taylor 1962) but so also does L_{oo}.

May, Pinhorn, Wells and Fleming (MS, 1964) found that the Bertalanffy parameters describing the growth of cod from various areas around Newfoundland did not follow the expected pattern and, whereas Taylor (1958) had described an increase in K with increase in temperature for cod over the general area of the Northeast Atlantic, these authors showed a decrease in K with decrease in latitude (the latter they regard equivalent to an increase in temperature) for the same species of fish over a large area of the Northwest Atlantic.

From the few authors referred to above it would seem that

(a) K is constant
L_{oo} is sensitive to changes in growth-rate
(Beverton and Holt 1957) (Theoretical).

(b) K increases as temperature increases
(Taylor 1958, 1959 and 1960)

(c) K increases as temperature increases
L_{oo} decreases as temperature increases but at a slower rate
(Theoretical) (Holt 1959)

(d) K increases as temperature increases } (Experimental)
L_{oo} increases as temperature increases } Kinne (1960)

(e) K decreases as temperature increases } May et al. (MS, 1964)
L_{oo} increases as temperature increases }

From the above considerations, one might suspect that the physiological attributes which make the Bertalanffy growth equation so attractive in bridging the gap between growth and metabolism are not as well established or understood as they might be. It seems preferable to avoid, for the time being at any rate, any possible physiological connotation which might be placed on the parameters of the Bertalanffy growth equation, and to treat this equation in a purely empirical manner. The equation provides a very good fit to the age at length data for redfish, as well as a convenient mathematical summary from which age and length values and growth-rates can be extracted with ease by simple calculation.

In the discussion above, it also seems clear that attempts at correlating K or L_{oo} with environmental factors do not necessarily lead to meaningful correlations between growth and the environment. This is possibly in part due to the over-riding importance that food is likely to have in affecting growth, for it would seem that the relative abundance or absence of food must dominate other environmental factors such as temperature (Brown, 1957); and in part due to the nature of the parameters themselves. As mentioned previously in Section 1, there is no parameter of growth-rate in the Bertalanffy equation and if growth in different populations is to be compared, it is really the growth-rate and how this varies from age to age in the different areas that must be

examined. Growth-rate in Bertalanffy type growth is a function which varies linearly with length and linearly with the logarithm of age. The slope of this line is in each case K and the intercept KL_{oo}, or a simple modification of this value. Thus the growth-rate at any age or length is determined by both K and L_{oo}. The parameter K does not, as is often inferred, directly represent growth-rate but the change in growth-rate per unit change in length (its dimensions are age^{-1} and not $length.age^{-1}$).

In considering the differences in growth-patterns between areas, it has thus been considered best to limit discussion to a consideration of how the growth-rates vary from area to area, and to consider only very briefly the possible correlations between Bertalanffy parameters and the environment.

7.22 Growth-rates of mentella redfish

7.221 Males

The Bertalanffy growth curves of male redfish from the 5 areas around Newfoundland reported here are plotted on the same coordinate system in Fig. 7.3. The parameters of these curves are shown in Table I.

In considering these growth curves, it should perhaps be recapitulated that the growth curves shown for Flemish Cap and Hamilton Inlet Bank represent the data from several widely separated depths, while the curves for the Southwest Grand Bank are derived from fish obtained in depths of less than 110 fathoms and those from Hermitage Bay and the Gulf of St. Lawrence from 140 and 129 - 142 fathoms respectively.

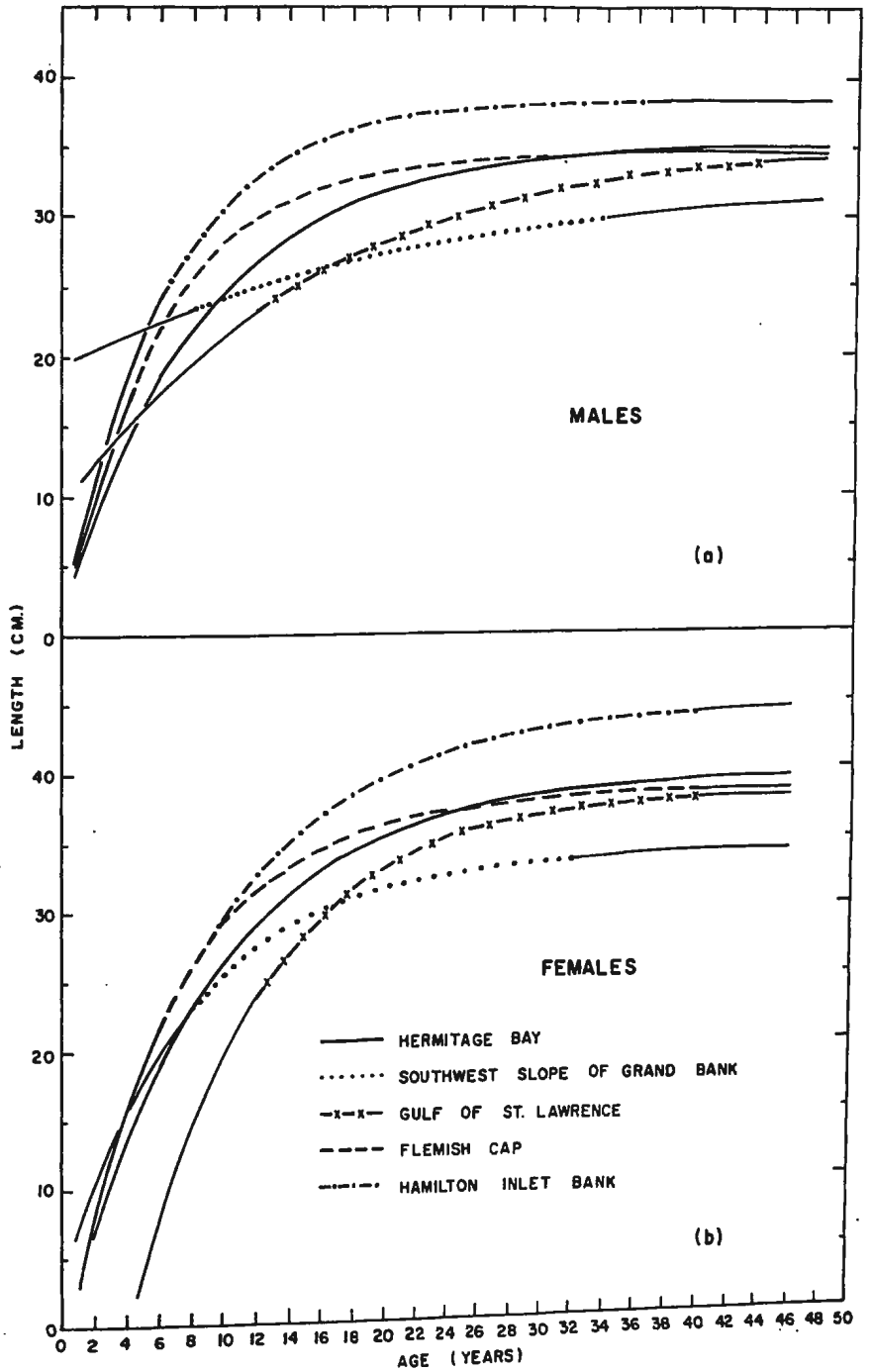

FIGURE 7.3 GROWTH CURVES OF *SEBASTES* REDFISH
(a) MALES
(b) FEMALES

From Fig. 7.3 (a), it seems likely that the male mentella of Hamilton Inlet Bank have a much faster growth-rate, and those of the southwest slope of the Grand Bank a slower growth-rate than the other areas. This is confirmed when the growth-rates are compared by length (Fig.7.4(a)). It is evident that until about a length of 32 cm, the growth-rates at any length are in the order of highest to lowest, Hamilton Inlet Bank, Flemish Cap, Hermitage Bay, Gulf of St. Lawrence and Southwest Grand Bank. However, when the growth-rates are compared in terms of age (Fig.7.5) we find that Hamilton Inlet Bank fish have fastest growth to about the age of 10, but at greater ages the fish from Hermitage Bay may be seen to be growing faster and, after the age of about 15 the fish of the Gulf of St. Lawrence lead the field. Apart from the Southwest Grand Bank fish, after about age 12 those from Flemish Cap show the slowest growth.

An examination of the Bertalanffy parameters and their 95% confidence limits indicates a complete overlap by K and t_o for all areas, and L_{oo} for Southwest Grand Bank and Gulf of St. Lawrence with the other areas. Hamilton Inlet Bank can be considered different from Hermitage Bay and Flemish Cap in the maximum length to which fish from these areas may attain.

7.222 Females

The area differences in growth pattern for female mentella parallel rather closely those of the males (Fig. 7.3b). Over the range of lengths corresponding to the ages for which we have fitted the Bertalanffy curves, (Fig.7.4 b), there are, relative to length, 3 main groups of growth-rate; the fish from Hamilton Inlet Bank, which show a fast growth-rate, and those from Hermitage Bay and the

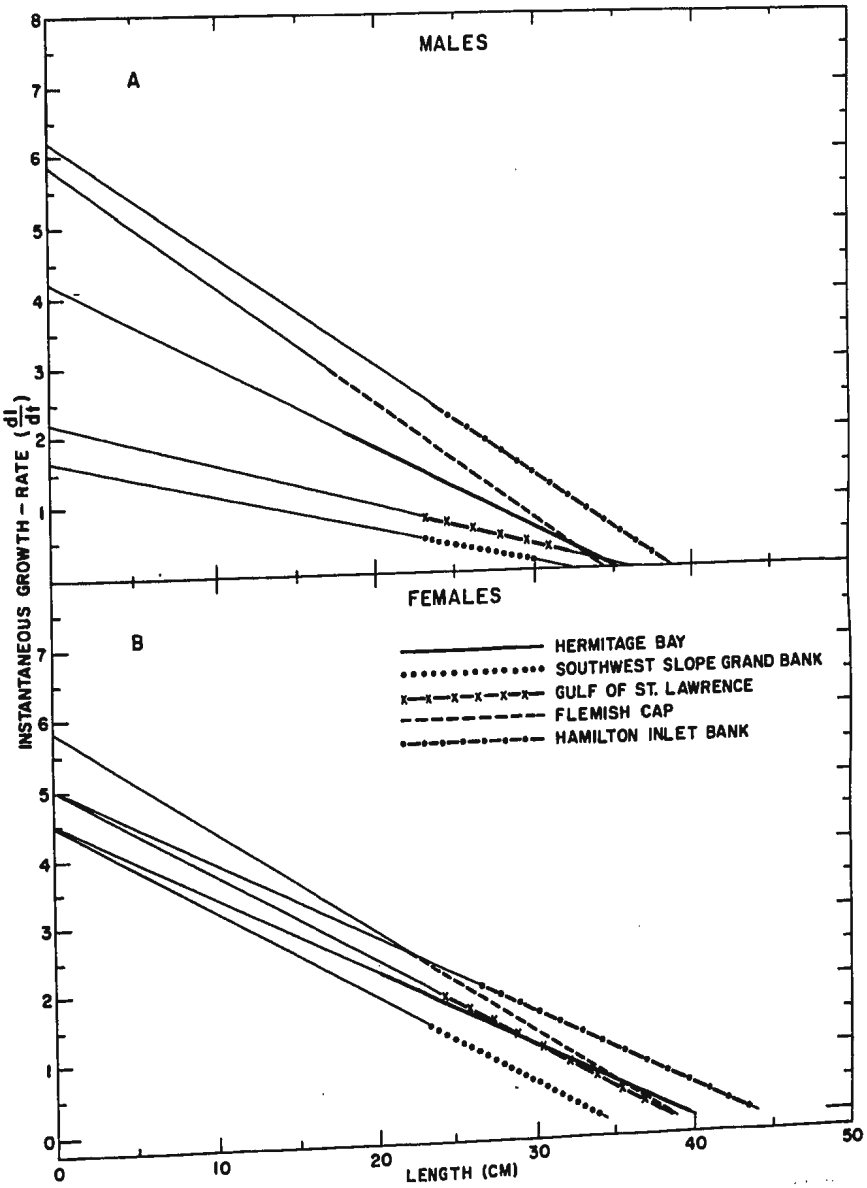

FIGURE 7.4 INSTANTANEOUS GROWTH-RATE AT EACH LENGTH - MERLUCCIUS

(a) MALES

(b) FEMALES

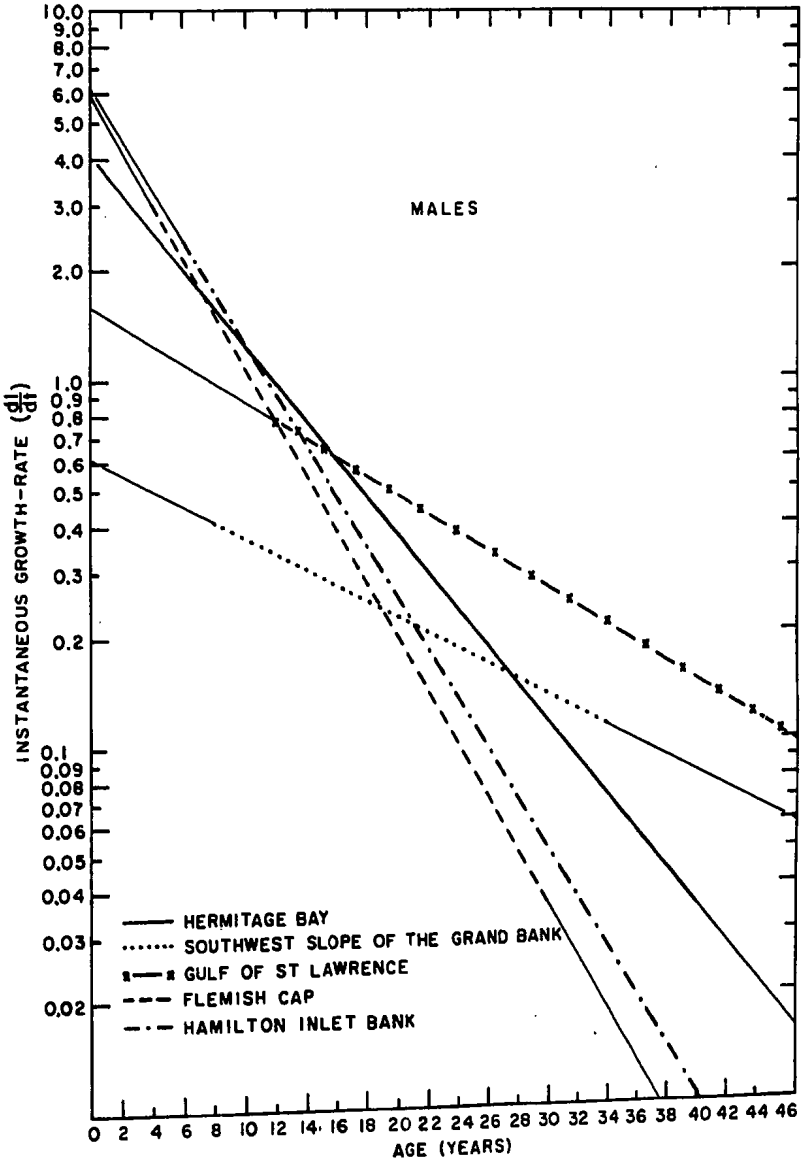

FIGURE 7.5 INSTANTANEOUS GROWTH-RATE AT EACH AGE - MENTELLA, MALES.

Gulf of St. Lawrence which show a medium growth-rate, and those from the southwest slope of the Grand Bank which show a slow growth-rate. Cutting across the fast and medium growing fish are those from Flemish Cap.

When the growth-rate is considered with respect to age (Fig. 7.6), the Gulf of St. Lawrence fish may be seen growing fastest till about the age of 28, and apart from these fish, Hamilton Inlet Bank fish grow fastest followed closely by those from Hermitage Bay.

An examination of the Bertalanffy parameters and their 95% confidence limits shows that the K and t_o may overlap from all areas, but that L_{oo} provides a likely separation of three differing growth patterns: Hamilton Inlet Bank having a high L_{oo}; Flemish Cap, Hermitage Bay and the Gulf of St. Lawrence having a medium L_{oo}; and the southwest slope of the Grand Bank having a low value for L_{oo}.

7.23 Growth-rates of marinus redfish

As marinus redfish were available from only two areas, the difference between the sexes is here considered as well and the growth curves shown in Fig. 7.7. The higher growth-rates for the Hamilton Inlet Bank area that we must suspect from this figure are confirmed, for the ages from which we have obtained the fitted curves, in Fig. 7.2, which shows that the growth-rates at each age are greater for both males and females in the Hamilton Inlet Bank area than they are at Flemish Cap.

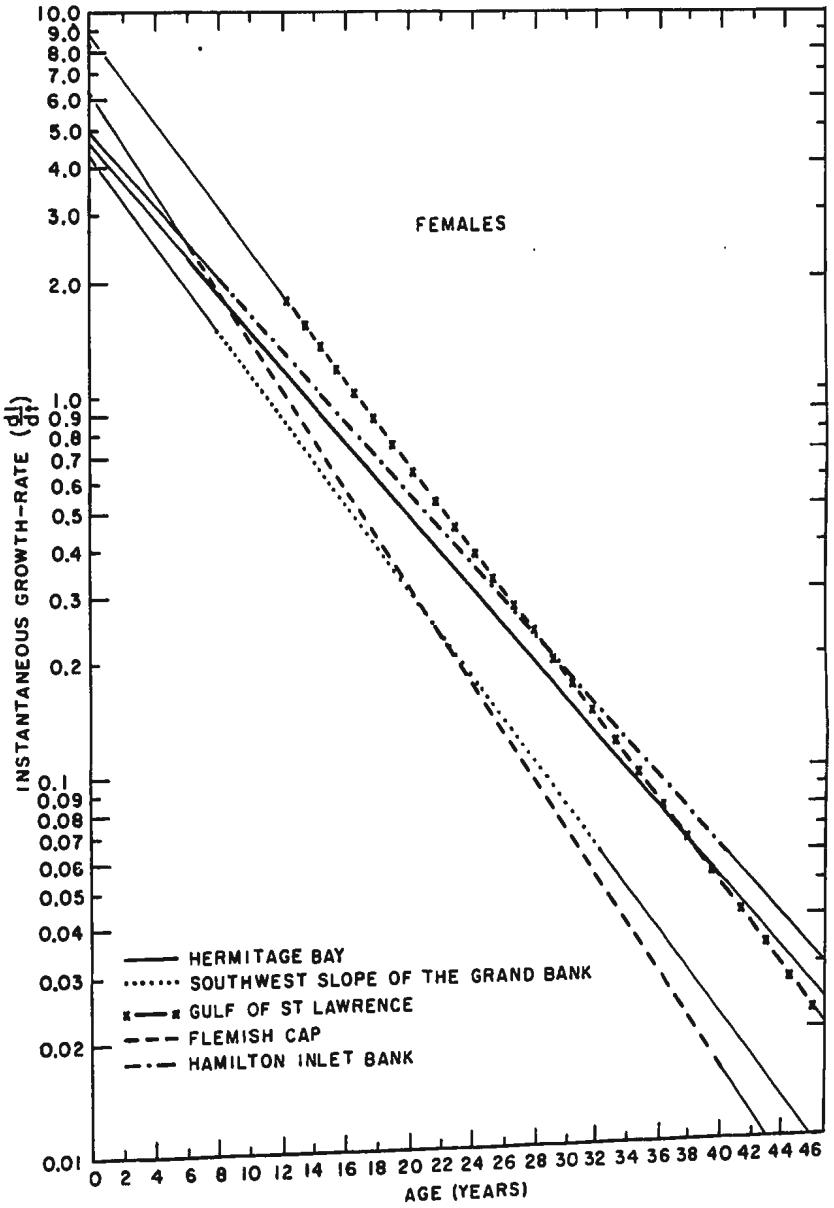

FIGURE 7.6 INSTANTANEOUS GROWTH-RATE AT EACH AGE - MENTELLA, FEMALES.

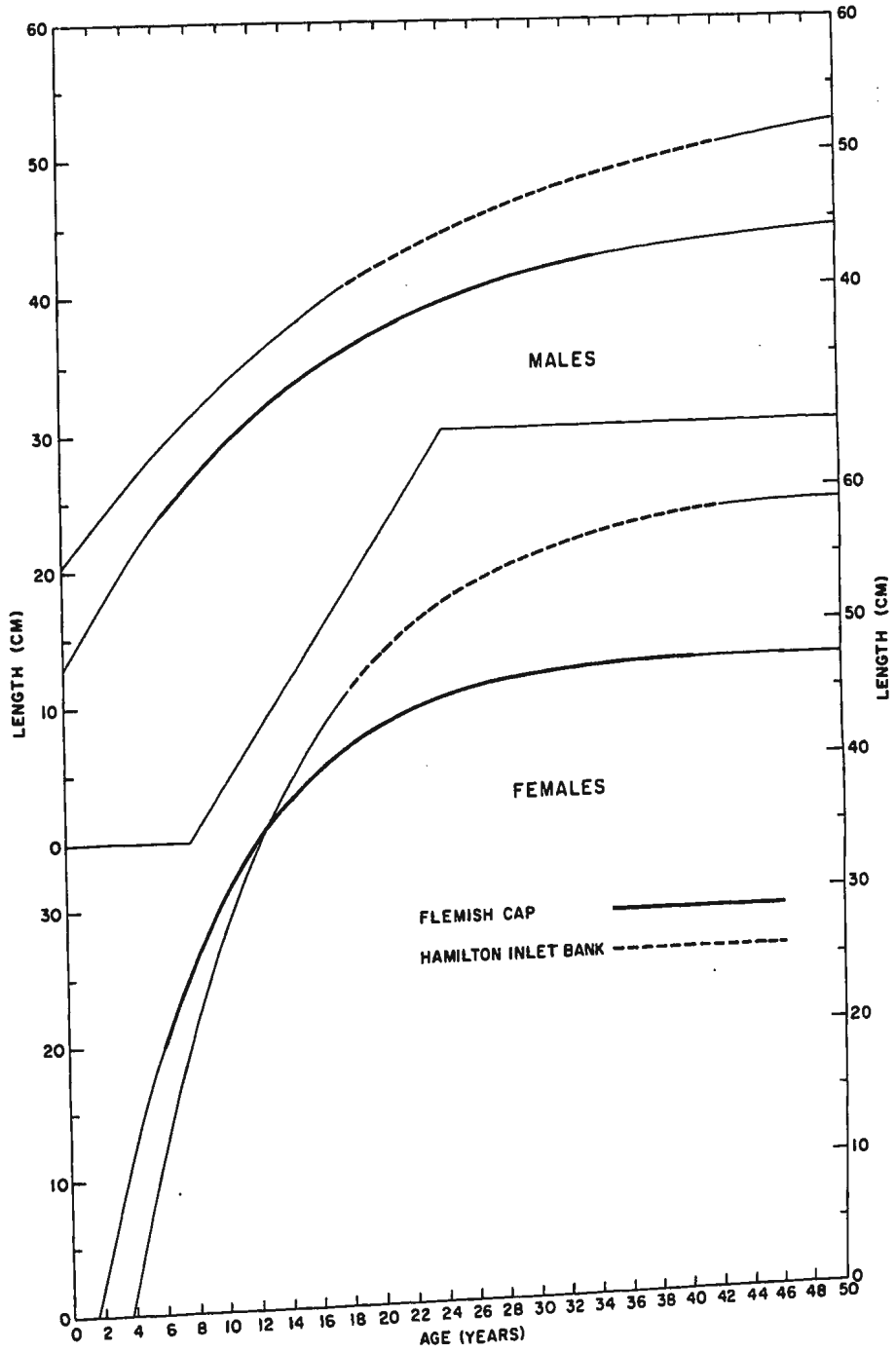

FIGURE 7.7 GROWTH CURVES OF MALE AND FEMALE MARINUS REDFISH FROM FLEMISH CAP AND HAMILTON INLET BANK.

8. Comparison of redfish growth curves as derived by different authors.

8.1 North American mentella redfish

8.11 General

Very little age-length data has been published for redfish of the ICNAF Area. Some data is available from the ICNAF Sampling Year Book but only from Russian sources and, apart from data gathered in 1961, this is summarised in a paper by Surkova (1962).

Perlmutter and Clarke (1949) were concerned primarily with immature redfish and, because much of their market sampling was aimed at these smaller fish, the values for mean length at age for the older fish in their samples are likely to be biased, with lower mean lengths and a flatter growth curve resulting.

Kelly and Wolf (1959) show growth curves of redfish from the Gulf of Maine for the years 1951, 1952 and 1953. Kelly and Wolf, while recognising the rather uncertain taxonomic position of the North American form of redfish, class the Gulf of Maine redfish, in their final table, as Sebastes marinus marinus. It is the author's opinion and that of Templeman (1959) that the Gulf of Maine redfish belong to the common North American mentella-type.

Canadian and United States length measurements are made to the nearest centimetre, from the anterior tip of the lower jaw, with the mouth closed, to the end of the mid-fork of the caudal fin. The Russian measurements, however, were of total length (to the tip of the caudal fin - Surkova, 1962) and presumably also made to the nearest centimetre.

(This does not seem to be stated anywhere, but Baranenkova (1957) shows a table of lengths from which one could infer that the measurements were to the nearest centimetre). Because of this difference in the basic dimension measured, we can expect that the Russian measurements will be larger than those of the United States and Canada. The difference will increase with size of fish and, according to Templeman (1959), should be about 1 to 1½ cm for redfish in the 30 to 40 cm length range.

The method of age estimation also differs between the United States and Canada on the one hand, whose biologists use otoliths, and Russian biologists who rely almost entirely on scales. In many species of fish it has been found that, although scales and otoliths agree and provide good age estimates for the younger fish, for the older fish which are forming very little new scale tissue annually, it becomes very difficult to distinguish between the winter and summer growth zones. This often results in an underestimation of the age of old fish by the scale method, as compared to the otolith method.

8.12 Hamilton Inlet Bank - ICNAF Division 2J.

From the ICNAF Division 2J (Fig. 1.1) we have data from Surkova (1962), and this may be compared with our data for Hamilton Inlet Bank (Section 6, this paper). Presented in Fig. 8.1 are Surkova's mean length at age data for fish collected in 1957 and 1958. His 1957 data are based on one rather small sample of fish taken in the same area as was our own, while the 1958 data are from several samples, most of which were obtained in the southern part of the ICNAF Division 2J.

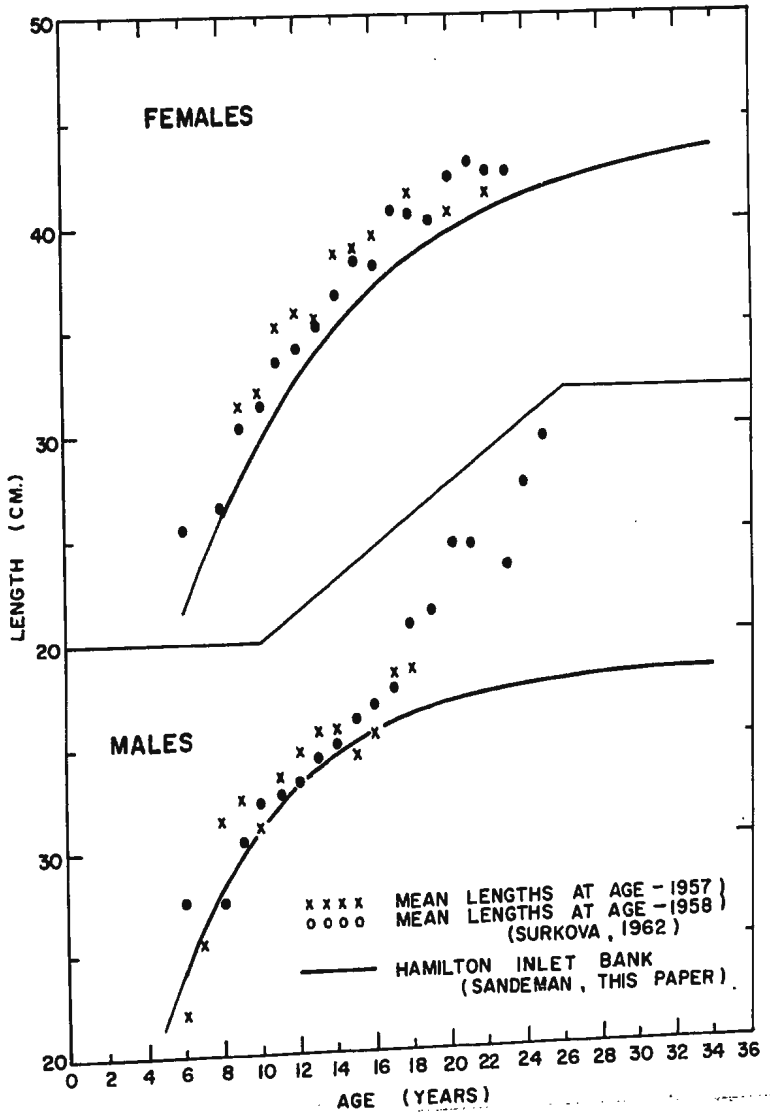

FIGURE 8.1 MEAN LENGTH AT AGE VALUES FOR SURKOVA'S (1962) DATA FROM ICNAF DIVISION 2J AND GROWTH CURVES FOR HAMILTON INLET BANK (SECTION 6, THIS PAPER) *MENTELLA*.

When these data points are compared with our fitted curves for the Hamilton Inlet Bank line, and allowance is made for the fact that the mean lengths of Surkova's data will be about one cm higher, it can be seen that, apart from the few very large males, the agreement between the growth curves is quite close.

Why the large males in Surkova's data should diverge so greatly from the general trend is not known. This could be due to the fact that scales have been used to obtain the age estimates, or alternatively to the mixing of some fish from the deeper fast-growing population with samples obtained mainly from shallower water.

8.13 Flemish Cap ICNAF Division 3M.

Surkova (1962) has presented age at length data for this ICNAF Division for the years 1956 to 1960. Surkova's mean length at age data for the years 1956 and 1959, the years from which our samples were obtained from the area of Flemish Cap, have been plotted in Fig. 8.2. Also shown in this figure are the Bertalanffy curves fitted to our own data (Section 5, this paper), and fitted to Surkova's data combined and averaged over the five years (unweighted).

The 2 sets of curves are widely different, with Surkova's data showing by far the faster growth-rate.

8.14 Southwest Grand Bank - ICNAF Division 3O

Shown in Fig. 8.3 are Surkova's mean length at age values for mentella redfish from ICNAF Division 3O in 1960 and the Bertalanffy curves fitted to our data from the southwest slope of the Grand Bank (Section 3, this paper). In comparing these

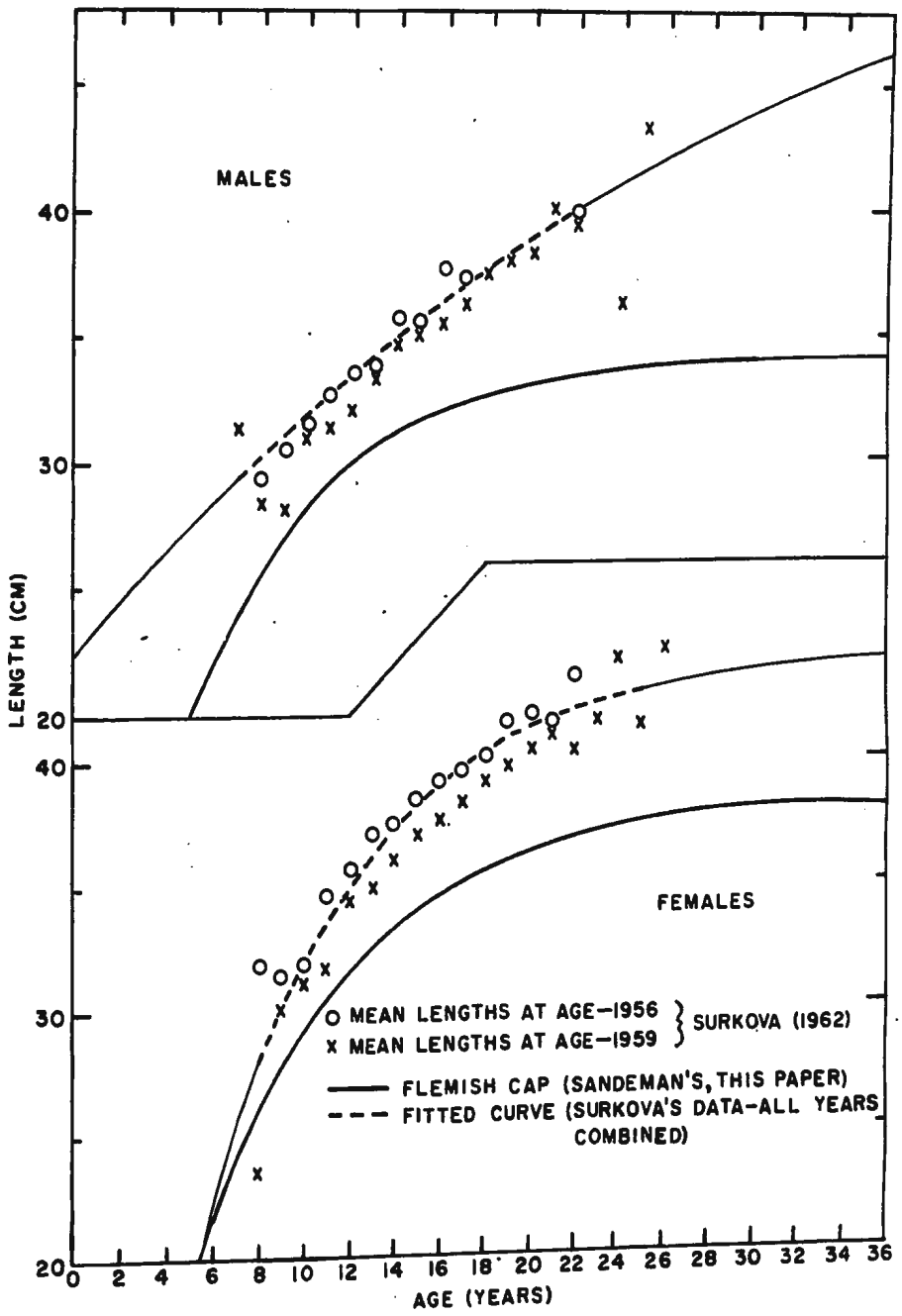

FIGURE 8.2 MEAN LENGTH AT AGE VALUES AND BERTALANFFY CURVES FITTED TO THE COMPLETE DATA FOR SURKOVA'S (1962) DATA FROM ICNAF DIVISION 3M AND GROWTH CURVES FOR FLEMISH CAP (SECTION 5, THIS PAPER) - MENTELLA.

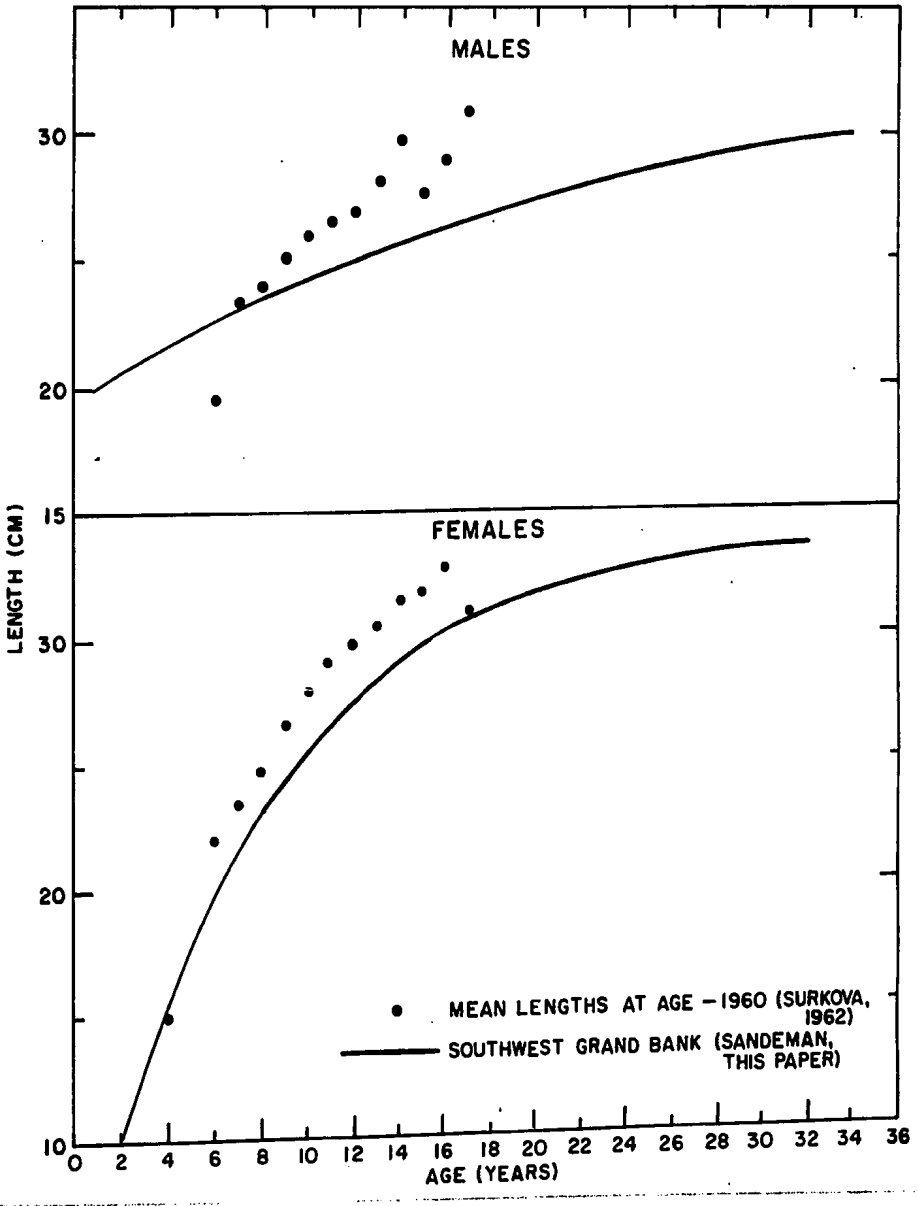

FIGURE 8.3 MEAN LENGTH AT AGE VALUES FOR SURKOVA'S (1962) DATA FROM ICNAF DIVISION 30 AND GROWTH CURVES FOR SOUTHWEST GRAND BANK (SECTION 3, THIS PAPER) - MENTELLA.

curves, it may be noted that agreement for the females is considerably closer than it was for the Flemish Cap area, and that the separation between the corresponding length at age values are about 2 cm for the younger fish and 3 cm for the older fish.

The difference between the age at length values for the males is exaggerated by the very flat curve that both Squires and Sandeman obtained for the male fish in the shallow water of the area in 1947.

8.15 Hermitage Bay - ICNAF Division 3P

Figure 8.4 shows Surkova's 1960 data for ICNAF Division 3P and the fitted Bertalanffy curves for our data from 3P (Hermitage Bay, Section 2, this paper). Once again Surkova's growth-rates are considerably faster.

8.16 Gulf of St. Lawrence

Steele (1957) has shown the results of age estimations from the otoliths of a small sample of 101 redfish taken in the Gulf of St. Lawrence. These results and the fitted Bertalanffy curves for our data from the area (Section 4, this paper,) are shown in Fig. 8.5. The difference between age estimates is very great indeed, and is likely due to differences in the basic method of age reading.

8.17 Gulf of Maine

Bertalanffy growth curves have been fitted for male and female redfish from the data of Kelly and Wolf (1959) for all samples collected in the Gulf of Maine in 1951, 1952 and 1953.

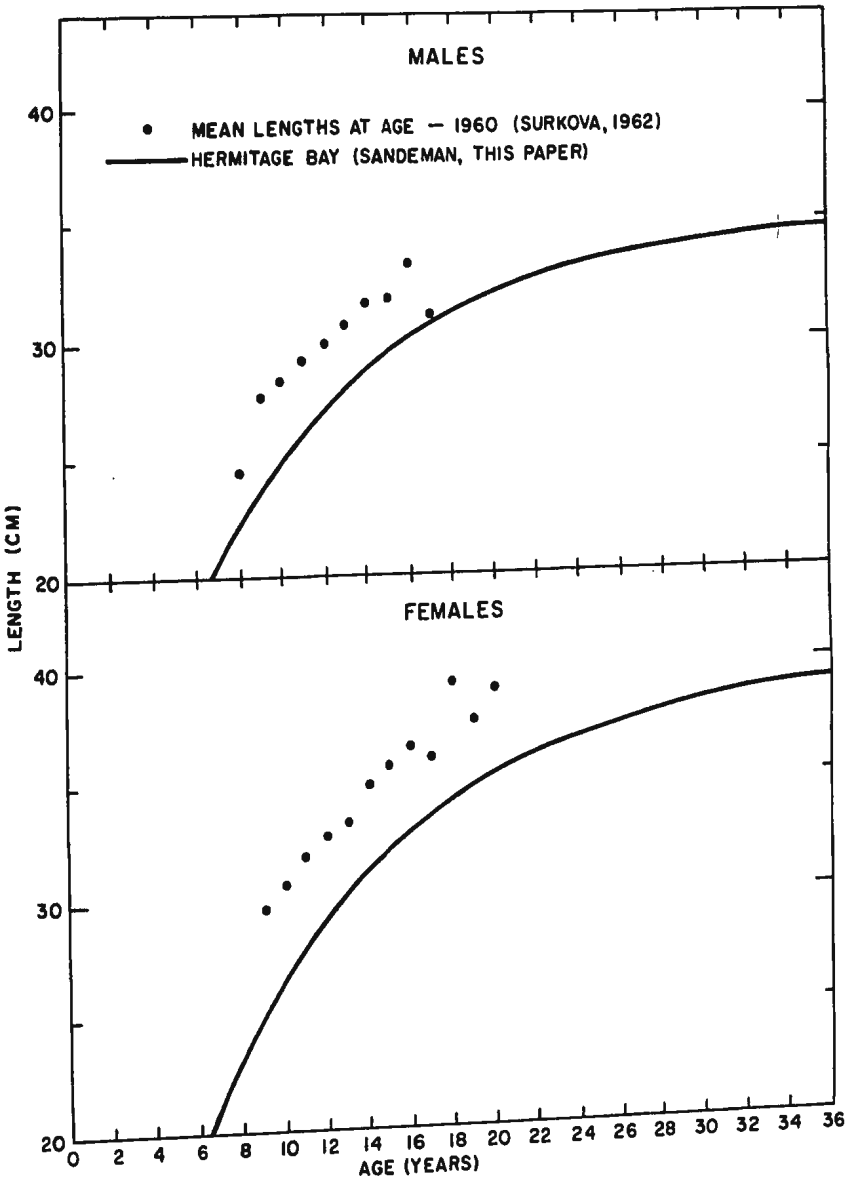

FIGURE 8.4 MEAN LENGTH AT AGE VALUES FOR SURKOVA'S (1962) DATA FROM ICNAF DIVISION 3P AND GROWTH CURVES FOR HERMITAGE BAY (SECTION 2, THIS PAPER) - MENTELLA.

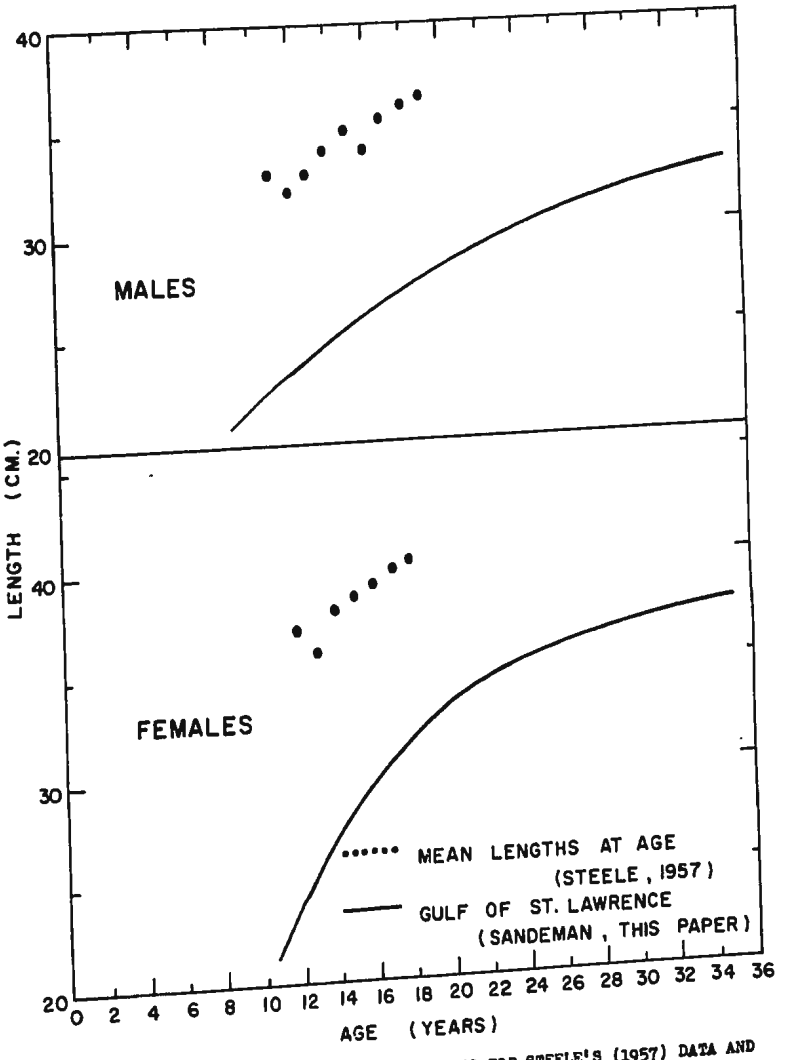

FIGURE 8.5 MEAN LENGTH AT AGE VALUES FOR STEELE'S (1957) DATA AND GROWTH CURVES FOR MENTELLA REDFISH IN THE GULF OF ST. LAWRENCE (SECTION 4, THIS PAPER).

The curves were fitted to the unsmoothed length at age data for ages 1 to 18, for both males and females. These curves, together with the mean length at age values to which they were fitted, are shown in Fig. 8.6. It is unfortunate that we have no age estimations for this area, but included in the figure are our Bertalanffy curves for Hermitage Bay. It is evident, both from the parameters of the fitted curves (below) and the curves themselves, that differences are not very great.

	Gulf of Maine		Hermitage Bay	
	Males	Females	Males	Females
L_{oo}	33.4	44.3	35.2	39.7
K	0.13	0.09	0.12	0.11
t_o	- 0.5	- 0.6	- 0.3	0.3

The curves for the males are practically coincident to an age of about 14 years, and after this the slightly higher value of L_{oo} for the Hermitage Bay curve exerts its influence, and causes the curves to gradually diverge. The curves for the females do not appear quite so similar as do those of the males, but the difference in mean length at each age is still less than 1.5 cm up to the age of 18, the largest age to which the curve was fitted. The Bertalanffy curve for the females of Hamilton Inlet Bank (Section 6, this paper) is also shown, and this provides an idea of how the curve for the data of Kelly and Wolf lies relative to the curves we have derived for various areas around Newfoundland.

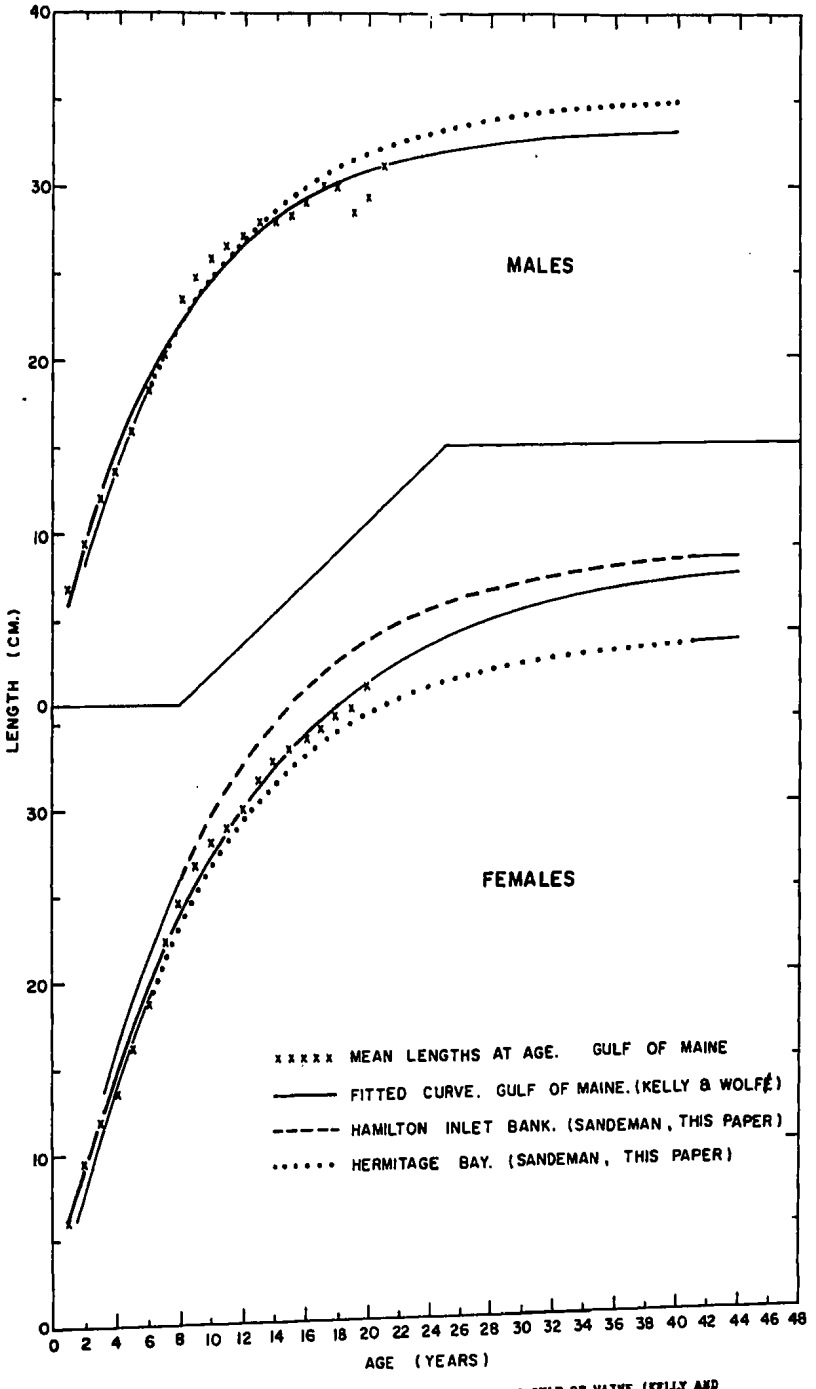

FIGURE 8.6 GROWTH CURVES OF MENTELLA IN THE GULF OF MAINE (KELLY AND WOLFE, 1959) COMPARED WITH THE GROWTH CURVES FOR MENTELLA FROM HERMITAGE BAY (SECTION 2, THIS PAPER) AND ALSO FOR THE FEMALES FROM HAMILTON INLET BANK (SECTION 6, THIS PAPER).

8.18 Discussion

In comparing the growth curves of Surkova with those of Samdeman, it seems most unlikely that the differences, which are so evident, could have been caused by between sample differences such as might exist due to the samples being obtained in diverse depths or localities. It is, in fact, difficult to evade the conclusion that the differences found between the results of these authors are due mainly to a difference in the basic method of age estimation. Thus, with otoliths being used by the one worker and scales by the other, the difference reduces to the much discussed controversy of scales versus otoliths in age determination.

Considerable effort has been spent in comparisons between the scale ages and otolith ages of many different species of fish, and the consensus of recent opinion has been overwhelmingly in favour of the use of otoliths for older fish.

Kohler, Templeman, Clark and Jensen (1958), who compared scale and otolith age determinations for each of 764 haddock, concluded that above 8 years of age the outer annuli are more easily distinguished in the otolith than in the scale, and that this led to a tendency for lower age estimates to be obtained for these older fish from scales than from otoliths. Furthermore, they conclude that for older, slower-growing stocks of haddock the otolith method will probably give more accurate results.

Saetersdal (1958), investigating the scales and otoliths of young haddock, found even in the very earliest years that a minority of the scales showed a complete lack of growth in a season of slow growth. His evidence suggests that the otolith

is a more sensitive recorder of the age of the fish than the scale. He also found, for arctic haddock, that in mature fish the outer growth zones of the otoliths are far more distinct and easier to identify than those of the scales, which may be completely lacking.

Rollefsen (1933) found that it was often not possible to discern the zones formed in the outer parts of the scales of the "skrei", while the corresponding otolith zones were particularly distinct. Schmidt (1955) had the same experience when studying the otoliths and scales of saithe, Gadus virens L. from Icelandic and Norwegian stocks. Trout (1958) also states that for gadoid populations, where the mean age is high, the otolith has been shown to give a more consistent age reading than the scale.

With redfish being such a slow growing species of fish and one which has, even using Surkova's age estimates, the mode of the age-frequency distribution at ages greater than 11 years in most of the areas around Newfoundland, it is difficult to see how scales could possibly provide ages approaching in accuracy to those obtained by otoliths. In this connection, it is interesting to note that the fish from Hamilton Inlet Bank yielded otoliths which were very much clearer and easier to read than any of the other areas and presumably the scales were similar; in this area was found the best agreement between the growth curves of Surkova and Sandeman.

In my examination of scales, I found them superior to otoliths for the first two or three years, but at ages greater than about seven years difficult to read with any confidence. The fact that Surkova can read scales to ages of 20 and more says much for her prowess at age reading.

Just as the lack of agreement between the growth-curves of Surkova and Sandeman emerges so clearly from the comparisons, so also does the presence of agreement between the curves of Kelly and Wolf (1959) for the Gulf of Maine and those discussed here for Hermitage Bay. Although the curves are for redfish from two different areas, it seems highly probable that the close agreement between the growth-curves reflects a real agreement with regard to the basic method of age determination. The most striking difference between the data presented by Kelly and Wolf (1959) and our data is the lack in the Gulf of Maine of the large, very old fish which seem so common in the samples from the Newfoundland area in 1947 - 1953. It seems probable that the high sustained fishing pressure to which the Gulf of Maine has been subjected has resulted in the relative absence of the large very old fish. In this connection, it is perhaps worth recapitulating that a similar dearth of these large old fish has been noted from the Gulf of St. Lawrence in recent years.

8.2 North American marinus redfish

Unfortunately the only data that has been published for marinus redfish in the ICNAF Area are from Subarea 1. Some age frequencies are shown in the ICNAF Sampling Yearbook, and Zakharov (1962) shows a table of age and mean length for marinus redfish from the same area. Unfortunately Zakharov's ages were determined from scales, and the growth-curve is typical of those obtained from scale readings. It is astonishing that Zakharov is able to read scales and obtain ages to as much as 39 years.

Travin's (1962) age frequency data also shows ages to 35 years, with 5 fish being classed as older than 35. In view of the basic discrepancy that appears between growth curves as derived from scales and otoliths of mentella redfish from the same area, it seems that little is to be gained by comparing, between different areas, marinus growth curves which have been derived from otolith or scale age determinations. As the available detailed data on age and growth from both mentella and marinus of the Northeast Atlantic (with the exception of Bratberg, 1955, 1956a and 1956b and Trout, 1961a who worked only with rather young fish; and Kotthaus, 1949, 1952 and 1958) were all from scale readings, it is unlikely that comparisons will be of any real value.

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10. References

Abramson, N. J. 1963. Computer programs for fisheries problems. Trans. Amer. Fish. Soc., 92 (3): 310.

Anon, 1957. Otoliths used to determine age of ocean perch. Comm. Fish. Rev., 19(5a): 6.

Baranenkova, A. S. 1957. [Material on the distribution of Ocean Perch genus Sebastes.] Dokl. Akad. Nauk. SSSR 113(2): 468 - 471.

Bertalanffy, L. von, 1934. Untersuchungen über die Gesetzlichkeit des Wachstums. 1. Teil. Allgemeine Grundlagen der Theorie; mathematische und physiologische Gesetzlichkeiten des Wachstums bei Wassertieren. Archiv. F. Entwicklungs mech., 131: 613 - 652.

1938. A quantitative theory of organic growth. (Inquiries on growth laws II). Human Biology 10(2): 181 - 213.

1949. Problems of organic growth. Nature 163: 156 - 158.

1957. Quantitative laws in metabolism and growth. Quart. Rev. Biol. 32(3): 217 - 231.

Beverton, R. J. H., 1954. Notes on the use of theoretical models in the study of the dynamics of exploited fish populations. U.S. Fish and Wildl. Serv., Fish. Lab., Beaufort, Misc. Contrib., no. 2. 181 pp. (Processed).

Beverton, R. J. H. and S. J. Holt, 1957. On the dynamics of exploited fish populations. Fish. Invest. Ser. II, xix. 1 - 533.

1959. A review of the lifespans and mortality rates of fish in nature, and their relation to growth and other physiological characteristics. Ciba Foundation Symposium on The lifespan of Animals, 1959, pp. 142 - 177.

Boldovskii, G. V., 1944. The food of the Norway Haddock in the Barents Sea. Trudy PINRO, 8: 307 - 330.

Brown, M. E., 1957. Experimental studies on growth. In The Physiology of Fishes. Vol I. pp. 361 - 400. Academic Press Inc. New York.

Bratberg, Erling, 1955. Vokser veren langsomt og er det mulig å bestemme dens alder. Fiskets Gang, Nr. 42: 552 - 555.

1956a. Om veksten og tydningen av de opake og hyaline soner i otolithene hos ikke Kjønnsmoden uer (Sebastes marinus L.) Fiskeridir. Småskr., Nr. 10, 1955.

1956b. On the interpretation of the opaque and hyaline zones in the otoliths of immature redfish (Sebastes marinus L.) J. Cons. Expl. Mer, 22(1): 66 - 74.

Collett, Robert, 1880. Sebastes marinus (L.) The Norwegian N. Atlantic Exped., 1876 - 1878, Zoology: Fishes. pp. 15 - 18.

Einarsson, Hermann, 1960. The fry of Sebastes in Icelandic waters and adjacent seas. Rit Fisk. 2(7): 1 - 67.

Ford, E., 1933. An account of the herring investigations conducted at Plymouth during the years from 1924 - 1933. J. Mar. Biol. Assoc., 19: 305 - 384.

Goode, G. B., and T. H. Bean. 1895. Deep-sea and pelagic fishes of the world. Special Bull. U.S. Nat. Mus., No. 2 pp 1 - 553 (+ atlas of 417 fig.)

Graham, H. W., 1953. United States research in Convention Area during 1952. ICNAF Ann. Proc., 3: 49 - 51.

1954. United States research in Convention Area during 1953. ICNAF Ann. Proc., 4: 56 - 59.

1955. United States research, 1954. ICNAF Ann. Proc., 5: 61 - 63.

1956. United States research, 1955. ICNAF Ann. Proc., 6: 64 - 67.

1957. United States research, 1956. ICNAF Ann. Proc., 7: 63 - 66.

Graham, Michael, 1929. The literature of age-determination of fish. Fish. Invest., ser. II, xi, No. 4: 1 - 50.

Graham, Michael, G. C. Trout, R. J. H. Beverton, John Corlett, A. J. Lee, and R. W. Blackler. 1954. Report on research from the Ernest Holt into the fishery near Bear Island, 1949 and 1950. Fish. Invest. Ser. II. 18(3): 1 - 87.

Gray, J., 1929. The kinetics of growth. J. Exp. Biol. 6: 248 - 274.

Hansen, Paul M. 1957. Redfish (Sebastes marinus) caught with shrimp trawl in West Greenland fjords, 1952 - 56. In Danish research report, 1956. ICNAF Ann. Proc., 7: 32 - 33.

1958(a) Redfish. ICNAF Ann. Proc., 8: 34.

1958(b) Redfish taken with the shrimp trawl in West Greenland fjords, 1952-1956. Conseil Expl. Mer, Ann. Biol., 13: 51 - 52.

1958(c) Length frequencies - redfish. ICNAF Sampling Yearbook (1955 and 1956), 1: 47 - 48.

1959. Length frequencies - redfish. ICNAF Sampling Yearbook (1957), 2: 73.

1961. Studies on the growth of the redfish (Sebastes marinus) in Godthåb Fjord, Greenland. ICNAF Sp. Publ. 3: 258 - 261.

1963. Tagging experiments on redfish (Sebastes marinus L.) in the Godthåb Fjord (W. Greenland). ICES. Distant Northern Seas Committee document (mimeographed).

Hansen, Vagn. Kr. and K. P. Andersen, 1961. Recent Danish investigations on the distribution of larvae of Sebastes marinus in the North Atlantic. ICNAF. Sp. Publ. No. 3: 201 - 215.

Hederström, Hans, 1759. Rön om Fiskars Ålder. Handl. Kungl. Vetenskapsakademin, Vol. xx: 222 - 229. Translation Observations on the Age of Fishes. Fish. Bd. Sweden, Inst. Freshwater Res. Drottningholm, Report No 40: 161 - 164.

Henderson, G. T. D., 1961a. Continuous plankton records: The distribution of young Sebastes marinus (L). Bull. Mar. Ecol., 5: 173 - 193.

1961b. Continuous plankton records: The distribution of young Sebastes marinus (L). ICNAF., Ann. Proc., 11: 103 - 110.

1962. Continuous plankton records: The distribution of young redfish in 1961. ICNAF, Redbook 1962, Part III: 43 - 46.

MS, 1963. Continuous plankton records: Studies on Redfish in 1962. ICNAF Annual meeting, 1963, Document No. 20. (Mimeographed).

Hoffbauer, C., 1899. Die Altersbestimmung des Karpfen an seiner Schuppe. Jahresbericht des Schlesischen Fischerei Vereins 23: 341 - 343.

Holt, S. J. 1959. Water temperature and Cod growth-rate. J. Cons. Expl. Mer, 24(2): 374 - 376.

1962. The application of comparative population studies to fisheries biology - an exploration. In The exploitation of natural animal populations. John Wiley and Sons. inc. New York, pp. 51 - 69.

Idelson, M. S., 1930. On the nourishment of the food fishes in the Barents Sea. Gidrobiol. Zhur.,SSSR, 8: 269 - 284.

Jensen, Ad. S., 1922. Sebastes marinus. Researches on the distribution, biology, and systematics of the Greenland fishes. Videns. Medd. Naturh. Foren. Kjöbenhavn, 74: 89 - 109.

Kashintsev, M. L., 1962. [Some notes on the food of redfish in the Newfoundland area.] Soviet Investigations in the Northwestern Atlantic VNIRO/PINRO. pp. 263 - 271.

Kelly, George F., and Robert S. Wolf, 1958. Age and growth of redfish, Sebastes marinus (Linnaeus), in the Gulf of Maine. ICNAF Spec. Publ., 1: 215 (Abstract).

1959. Age and growth of redfish, Sebastes marinus (Linnaeus) in the Gulf of Maine. U.S. Fish and Wildl. Serv., Fish. Bull., 60(156): 1 - 31.

Kelly, G. F. and A. M. Barker, 1961. Ovservations on the behaviour, growth, and migration of redfish at Eastport, Maine. ICNAF Sp. Publ. 3: 263 - 278.

1963. Effect of tagging on redfish growth-rate at Eastport, Maine. ICNAF Sp. Publ. 4: 210 - 213.

Kinne, Otto, 1960. Growth, Food intake, and food conversion in a euryplastic fish exposed to different temperatures and salinities. Physiol. Zool. 33(4): 288 - 315.

Knight, William, MS 1962. Groundfish sampling studies. Fish. Res. Bd. Canada, Biological Station, St Andrews, Original manuscript No. 940. (Unpublished).

Kohler, A. C., W. Templeman, J. R. Clark and A. C. Jensen. 1958. Haddock scale-otolith comparisons. ICNAF Sp. Publ., 1: 199.

Kotthaus, Adolf. 1949. Alter und Wachstum beim Rotbarsch. Fischereiwelt 1(5): 68 - 69.

1952. Ökologische und fischereiwissenschaftliche Untersuchungen über den Rotbarsch (Sebastes marinus L.) II. Zur Altersbestimmung beim Rotbarsch. Ber. Deutschen wiss. Komm. Meeresforsch., N.F., 12(4): 503 - 511.

1958. Age and growth of redfish, Sebastes marinus (L.) ICNAF Sp. Publ. 1: 217 - 222.

Kotthaus, Adolf, and Gerhard Krefft. 1957. Fischfaunenliste der Fahrten mit F.F.S. Anton Dohrn nach Island-Grönland. Ber. deutschen wiss. Komm. Meeresforsch. N.F., 14(3): 169 - 191

Lambert, D. G., 1960. The food of the redfish Sebastes marinus (L). in the Newfoundland area. J. Fish. Res. Bd. Canada, 17(2): 235 - 243.

Lundbeck, Johs, 1940. Rotbarsch-Goldbarsch-Tiefenbarsch. Deutsche Fischerei-Rundschau, 63(2): 32 - 33.

Magnusson, Jakob, 1955. Mikroskopisch-anatomische Untersuchungen zur Fortpflanzungsbiologie des Rotbarsches (Sebastes marinus Linné). Z. Zellforsch., 43: 121 - 167.

Marty, J. J. 1958. U.S.S.R. investigations in the Convention area during recent years. ICNAF Annual Meeting, 1958, Doc. No. 34, Ser. No. 563, (mimeographed).

May, A. W., A. T. Pinhorn, R. Wells and A. M. Fleming. MS, 1964. Cod growth and temperature in the Newfoundland Area. ICNAF Environmental Symposium, Contribution No. D.6: 1 - 23.

Medawar, P. B., 1945. Size, shape and age. In, Essays on growth and form pp. 155 - 187. Clarendon Press, Oxford.

Murray, Sir John, and Dr. Johan Hjort, 1912. The depths of the ocean. Macmillan and Co., London, 821 pp.

Nansen, F. 1886. De Norske Fiske. Norsk Fiskeritidende 5 Aarg., p. 73.

Parrish, B. B. 1958. Comparison of European and North American techniques of measuring nets, of reading ages of fish and of studying growth. Convenor's Report, Working Party VI. Symposium held at Biarritz, France, 1956. ICNAF Sp. Publ., 1: 113 - 138.

Perlmutter, Alfred, and George M. Clarke. 1949. Age and growth of immature rosefish (Sebastes marinus) in the Gulf of Maine and off western Nova Scotia. U.S. Fish & Wildl. Serv., Fish. Bull., 51(45): 207 - 228.

Pimentel, Gomes, Frederico, 1953. The use of Mitscherlich's Regression Law in the analysis of experiments with fertilizers. Biometrics 9(4): 498 - 516.

Pimental-Gomes, Frederico and Euripedes Malavolta 1949. Aspectos matematicos e estatisticos de Lei de Mitscherlich. Anais Esc. Sup. Agr. "Luis de Queiroz", 6: 193-229.

Raitt, D. F. S., MS, 1962. Scottish redfish larval investigations 1962. ICES Distant Northern Seas Committee, Paper No. 81, 1962. (Mimeographed).

Rasmussen, Birger. 1958. Notes on the otoliths of S. marinus and S. viviparus. ICNAF Sp. Publ., 1: 223 - 225.

Rees, E. I. S. MS, 1962. Food and feeding of redfish in Hermitage Bay. Fish. Res. Bd. Canada, Ann. Rept. Biol. Sta., St. John's, Nfld., for 1961 - 62: 67 - 72.

Reibisch, J. 1899. Ueber die Eizahl bei Pleuronectes platessa und die Altersbestimmung dieser Form an den Otolithen. Wiss. Meeresunt., Kiel, IV: 233 - 248.

Richards, F. J., 1959. A Flexible Growth Function for Empirical Use. J. Exp. Bot. 10(29): 290 - 300.

Ricker, W. E., 1958. Handbook of computations for biological statistics of fish populations. Bull. Fish. Res. Bd. Canada, No. 119: 1 - 300.

Rollefsen, Gunnar. 1933. The otoliths of the cod. Rep. Norweg. Fish and Mar. Invest., 4(3): 1 - 14.

1935. The spawning zone in cod otoliths and prognosis of stock. Rep. Norweg. Fish and Mar. Invest., 4(11): 1 - 10.

1961. Chairman's report, Section V. Age and Growth, ICES/ICNAF Redfish Symposium. ICNAF Sp. Publ. 3: 253.

Saemundsson, B., 1932. Sebastes marinus (Linné 1761) and Sebastes viviparus (Krøyer 1844). Faune Ichthyologique de l'Atlantique Nord, Copenhague, No 10.

Saetersdal, G. 1958. Use of otoliths and scales of the arctic haddock. ICNAF Sp. Publ., 1: 201 - 206.

Sandeman, E. J., 1957. Redfish grow slowly. Fish. Res. Bd. Canada, Atl. Prog. Rept., No. 67, pp. 26 - 28.

1958. Growth of young redfish. ICNAF, Spec. Publ., 1: 227.

1961. A contribution to the problem of the age determination and growth-rate in Sebastes. ICNAF Sp. Publ. 3: 276 - 283.

Schmidt, U., 1955. Beiträge zur Biologie des Köhlers (Gadus virens L.) in den Isländischen Gewässern. Ber. deutschen wiss. Komm. Meeresforsch., N.F., 14(1): 46 - 82.

Smaragdova, N. P., 1936. [Growth of Sebastes marinus L. in the Barents Sea.] Bull. Soc. Nat., Moscow, Sect. Biol., 45(5): 331 - 337.

Sorokin, V. P., 1958. [The reproductive biology of the redfish, Sebastes marinus L. and Sebastes mentella. Travin in the Barents and Norwegian Seas.] Trudy Soveshch. Fiziol. Ryb. 1956: 158 - 170.

1961. The redfish, gametogenesis and migrations of the Sebastes marinus (L.) and Sebastes mentella Travin. ICNAF Sp. Publ. No. 3: 245 - 250.

Steele, D. H., 1957. The redfish (Sebastes marinus L.) in the western Gulf of St. Lawrence. J. Fish. Res. Bd. Canada, 14(6): 899 - 924.

Stevens, W. L., 1951. Asymptotic regression. Biometrics 7(3): 247 - 267.

Surkova, E. I., 1957. [Sex and age composition of the redfish (Sebastes mentella Travin) of the Kopytov area.] Trudy PINRO, 10: 172 - 185.

1961. Redfish, Growth and Age. ICNAF Spec. Publ., 3: 285 - 290.

1962. [Size and age composition of redfish (Sebastes mentella Travin) from the North-west Atlantic.] Soviet Investigations in the North-western Atlantic VNIRO/PINRO pp. 297 - 311.

Tåning, Å. V., 1949. On the breeding places and abundance of the redfish (Sebastes) in the North Atlantic. J. Conseil Expl. Mer, 16(1): 85 - 95.

1951. Fish-fry in West Greenland waters, July, 1950. Redfish (Sebastes marinus). Ann. biol., Copenhague, 7: 40.

Taylor, C. C., 1958. Cod growth and temperature. J. Cons. Expl. Mer, 23: 366 - 370.

1959. Temperature and growth - the Pacific razor clam. J. Cons. Expl. Mer, 25: 93 - 101.

1960. Temperature, growth and mortality - the Pacific cockle. J. Cons. Expl. Mer, 26: 117 - 124.

1962. Growth equations with metabolic parameters. J. Cons. Expl. Mer, 27(3): 270 - 286.

Templeman, Wilfred, 1954. Summary of Canadian groundfish research in the Convention Area During 1953. Subarea 3. ICNAF Ann. Proc., 4: 23 - 25.

1959. Redfish distribution in the North Atlantic. Fish. Res. Bd. Canada, Bull. No. 120, pp. 1-173.

Templeman, Wilfred, 1961. Redfish distribution off Baffin Island, Northern Labrador, and in Ungava Bay in August - September 1959. ICNAF Spec. Publ., No 3: 157 - 162.

Templeman, W., and E. J. Sandeman, 1957. Two varieties of redfish in the Newfoundland area. Fish. Res. Bd. Canada, Atl. Prog. Rept., No. 66, pp. 20 - 23.

1959. Variations in caudal pigmentation in late-stage pre-extrusion larvae from marinus- and mentella-type female redfish from the Newfoundland area. J. Fish. Res. Bd. Canada, 16(6): 763 - 789.

Tomlinson, P. K. and N. J. Abramson, 1961. Fitting a von Bertalanffy growth curve by least squares. State of Calif. Dept. Fish and Game, Fish Bull., No. 116: 1 - 69.

Travin, V. I. 1951. [A new species of redfish in the Barents Sea, (Sebastes mentella Travin, sp. nov.)] Doklady Akad. Nauk S.S.S.R., 77(4): 741 - 744.

1959. Union Soviet Socialist Republics Research Report, 1958. ICNAF Ann. Proc., 9: 81 - 85.

1962. Age frequencies - redfish. ICNAF Sampling Yearbook 5: 54.

Travin, V. I., K. Janoulov, A. Postolaky, and G. Zaharov. 1961. Redfish stock distribution in the ICNAF area. U.S.S.R. Research Report, 1960. ICNAF., Ann. Proc., 11: 87 - 89.

Trout, G. C. 1954. Otolith growth of the Barents Sea cod. Cons. Expl. Mer, Rapp. et Proc. -Verb., 136: 89 - 102.

1958. Otoliths in age determination. ICNAF Sp. Publ. 1: 207 - 214.

1961. The growth of immature Sebastes viviparus (Krøyer) from the north Norwegian coast. ICNAF Sp. Publ., 3: 291 - 296.

1961(a). The otolith of group-0 Sebastes mentella Travin. ICNAF Sp. Publ., 3: 297 - 299.

Van Oosten, John, 1929. Life history of the lake herring (Leucichthys artedi Le Sueur) of lake Huron as revealed by its scales, with a critique of the scale method. Bull. U.S. Bur. Fish. 44: 265 - 428.

Verrill, A. E., 1871. On the food and habits of some of our marine fishes. Amer. Nat. 5: 397 - 400.

Veshchezerov, V. V. 1944. [Some materials on the biology and fisheries of Norway haddock (Sebastes marinus) of the Barents Sea.] Trudy PINRO 8: 236 - 270.

Walford, L. A., 1946. A new graphic method of describing the growth of animals. Biol. Bull., 90(2): 141 - 147.

Zakharov, G. P. 1962. [On the biology of redfish (Sebastes marinus L.) in West Greenland. Soviet Investigations in the North-western Atlantic.] VNIRO/PINRO pp. 319 - 330.

MS, 1963. Redfish above the oceanic depths ICNAF Annual meeting, 1963, Document No. 55 (mimeographed).